ANATOMICAL and PHYSIOLOGICAL STUDIES

in RHODODENDRON

by

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C O N T E N T S.

I. INTRODUCTION

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REVIEW of LITERATURE.

The morphology of the genus Rhododendron has not up to the present been dealt with in any completeness, although workers on the whole Order Ericaceae, or single Sub-orders, have recorded various morphological features at different times. The seedling of Rhododendron arboreum was briefly described by LUBBOCK (13) in 1892, and a number of seedlings also by BAYLEY BALFOUR (1) in 1917; these writers however confined themselves to external morphological characters, and so far there has been no record of the anatomical structure of the seedling. Isolated references and descriptions of characteristic anatomical features in the adult plant occur in numerous papers. In 1870, for example, GRIS (7) described the heterogeneous pith of many Dicotyledons including Rhododendron. VESQUE (24) in 1875, noted the occurrence of a pericyclic phellogen in Rhododendron and a number of other plants. Mycorrhizal infection in members of the Ericaceae, including Rhododendron ponticum and Azalea indica, was recorded by FRANK (6) in 1887, and the general appearance of the infecting fungus described. The earliest paper, however, treating of the anatomy of Rhododendron in any detail is a later one by VESQUE (25, 1885), dealing with the characters of some Gamopetalous orders based on their leaf-anatomy. In

this he describes the structure of several types of hair and the general anatomy of the leaf of about fourteen species of Rhododendron, grouping them according to different structural features. A comprehensive and interesting account of the leaf structure of the Rhododendroideae, based on the anatomical features of over forty species of Rhododendron, was published by BREITFELD (2) in 1888. There remains to be mentioned a contribution of SIMON (20, 1891) on the comparative anatomy of the Epacridaceae and Ericaceae, where he touches briefly on a few anatomical points observed in Rhododendron. SOLEREDER (22) has summarised most of the anatomical work done on the genus up to the time of his publication (1908).

DESCRIPTION OF THE GENUS.

The Order Ericaceae represents the most primitive order in the Gamopetalae, and shows indications of active evolutionary trends within it, as instanced by the tendency to reduction of floral parts, and a progressive trend from an arborescent to a low-growing shrubby form. Both these trends are exhibited in the genus Rhododendron, which is by far the largest genus in the Order, and comprises nearly 1200 species. Its chief centre of distribution occurs in the Himalayas and the mountains of South-west China, but there are also many species native to Japan and Korea, North America, New Guinea, Malaya and Indo-China. A

few alpine forms are found also in the mountains of Central Europe. All the species are woody, the habit of the plant ranging from low-growing alpine shrubs to arborescent forms attaining a considerable height. Most of these are evergreen, the leaves in the majority of species showing well-marked xerophytic characters; all are simple in outline, and many are leathery in texture, possess a thick indumentum, and show marked leaf-rolling. The shape of the leaf, the characteristic indumentum and the presence or absence of peltate scales are important characters in the identification of species.

AIM OF THE INVESTIGATION.

The present work was undertaken with a view to investigating in detail the anatomy of some species of the genus in their seedling and adult forms. It was hoped that the problem of how far adult peculiarities are exhibited in the seedling might be elucidated for this genus, and that a detailed examination of the vegetative organs might reveal anatomical features which would prove of systematic value.

Taking into consideration the diagnostic importance attached by some authors to the seedling structure, and the distinctive anatomical characters shown in the leaves of members of the Ericaceae, most of the present work has been concerned with these two lines of research.

MATERIAL AND METHODS.

The material used for these studies has been almost entirely Himalayan, Chinese or Japanese, although a few Javanese species were also included. Nearly 100 species were examined for seed characters, 70 for germination, and nearly 50 for seedling anatomy, R. decorum being taken as the type throughout. All the seeds used for Section II were collected in the Royal Botanic Garden, Edinburgh, and were sown during March and April.

Except when examined in a fresh state, the material used throughout the work was fixed in Blé's fixative, of the following composition:

70% alcohol	90 parts by volume
40% formalin	7 " " "
Glacial acetic acid	3 " " "

The material was then washed in 70% alcohol, and preserved in this or in 95% alcohol. Various combination stains were used for the sections, including safranin and light green, safranin and haematoxylin, and gentian-violet and eosin.

The seedling anatomy was examined from microtome sections, 8 - 10μ in thickness. The seedlings were embedded in paraffin of medium melting-point (48° - 50° C); clove oil was substituted for xylol as a clearing agent on account of its rendering the seedlings less brittle.

More than 100 species were cut and examined for

Section III. The nodal anatomy was examined entirely from hand sections of fresh material, the combination stain of phloroglucin and HCl being employed to detect the course of the vascular tissue. For examination of the leaf tissues 50 species, representing as many series as possible, were used, a small central portion being cut from each leaf, embedded in paraffin and stained with safranin and light green. Penetration of the tissues was often found to be difficult, especially in large leaves possessing a thick indumentum, and for these hand sections from fresh material were made. 100 species were examined for Section IV, Sudan III being employed throughout for the detection of the endodermal and cork tissues.

The material used throughout the investigation was obtained from the Royal Botanic Garden, Edinburgh, by the courtesy of Professor Wright Smith and his staff, to whom the writer wishes to acknowledge her deep indebtedness.

II. THE SEED AND SEEDLING.

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A. THE SEED AND GERMINATION.

The seed.

The seed of Rhododendron is always very small, though different species show considerable variation in size. The size within a species is however fairly constant. The seed is flattened and ovoid in shape, the micropylar end being slightly pointed. It is enclosed in a tough brown testa which in some species is expanded in one plane to form a membranous wing round the seed (Fig. I b,d). In others this expansion is confined to one end, or sometimes both ends, of the seed where it forms a small tuft (Fig. I c,f). Some species however show little or no projection of the testa. The Vaccinioides type of seed, which includes the Javanese species, differs from the rest in having a much elongated expansion of the testa at each end of the minute seed. Each of these expansions may measure sometimes twice the length of the seed itself (Fig. I a.). The colour of the testa varies in different species from a pale yellow to a blackish brown. The cells are large and much elongated, with thickened lateral walls and tapering ends. Extremely numerous fine pits are distributed over the entire outer surface of the testa (Fig. II). The seed is endospermic, the main food reserve being oil; protein is also present. The cells of the endosperm are large and polygonal in shape with prominent nuclei. The

embryo is straight and lies extended in the direction of the long axis of the seed (Fig. III). The cotyledons are very small, with their upper surfaces contiguous enclosing the plumule. The hypocotyl and radicle are unusually long and rather slender.

Germination.

When a sowing is made the seeds should be placed on the surface of the soil and left uncovered. This enables the young seedling to commence assimilation before the small food reserve of the seed is exhausted. The germination is epigeal and takes place usually 3-4 weeks after sowing. The radicle emerges from the micropylar end of the seed and sometimes shows a marked red colour at its apex. It is followed by the hypocotyl which elongates, thus drawing the cotyledons out of the seed coat. There is little or no arching of the hypocotyl behind the plumule on account of its position on the surface of the soil (Fig. IVa,b). As the hypocotyl lengthens it turns upwards through an angle of 90°, and the seedling at this stage often exhibits a double curvature in the central part of its axis, due to the positively and negatively geotropic movements of root and shoot respectively (Fig. IV c). The seed-coat adheres to the tips of both cotyledons for a considerable time after the hypocotyl has straightened out, and for a still longer period to one cotyledon after they are fully expanded (Fig. IV d).

B. THE YOUNG SEEDLING.

i) External Morphology.

The Cotyledon.

At the age of 5-6 weeks after sowing the seedling stands about 6mm. above the ground. The cotyledons are now fully expanded but have not attained their maximum size. They are very small, varying in length from 3-4 mm. in R. discolor to 1 mm. or less in R. triflorum, R. oleifolium and others. They are simple in outline and shortly petiolate. Small buds are formed in the cotyledonary axils; these may develop later into short branches but usually remain dormant. The shape of the cotyledon varies considerably; in some species it is broad and obtuse, and in others long and narrow or ovate with a pointed apex. The upper and lower surfaces of the cotyledon are glabrous except in rare cases where a few capitate or peltate hairs occur on the upper surface. The former are seen in R. decorum, and the latter infrequently on cotyledons of R. villosum. The margins are in the majority of cases entire, but may sometimes bear a number of short, thick hairs which are colourless and easily visible to the naked eye (e.g. R. arboreum, R. decorum). The cotyledons possess a definite midrib from which lateral veins arise alternately. A few weeks after germination a pink or red colour often appears in the hypocotyl and sometimes on the lower surface of the cotyledons. This colour, which

is due to the presence of anthocyanin in the outer tissues of the seedling, is usually most intense in the upper hypocotyl, and is sometimes present also in the tiny plumule. It may persist for an indefinite period in the seedling, but usually disappears after a short while. The pigment is present in solution in many of the cortical cells in the hypocotyl, and in the outer spongy mesophyll cells of the cotyledon. When present in the epicotyl, the colour is distributed throughout the small cells of the cortex and pith, but does not occur in the large thin-walled elements of either of these tissues.

BAYLEY BALFOUR in his Observations on Rhododendron Seedlings found that the development of anthocyanin in the leaves of juvenile plants is associated with various forms of indumentum in the leaves of the adult and points out that, apart from this genus, the association of pigmentation with woolly or hairy surfaces is rare.

The Hypocotyl and Root.

The hypocotyl is terete and may be sturdy or very slender, measuring 1 mm. or less in diameter. It is in all cases glabrous and pale green or pink in colour. The root system of the young seedling is relatively large, and consists of a very fine tap-root, 2 cm. or more in length. A few short lateral roots are sometimes present (Fig. IVd,e), but there is an absence of root-hairs, the plant being mycorrhizal

in habit.

ii) Teratological Seedlings.

Teratological seedlings of various kinds are of frequent occurrence in Rhododendron. Monocotylous seedlings have been found (e.g. in R. Cooperi and R. Tschonoskii), but are extremely rare. In these the stelar arrangement of the root and hypocotyl is normal in possessing two phloem strands. Only one trace, however, passes out into the single cotyledon, the other bundle remaining 'in situ' in the stem (Fig. V). The anatomy of the hypocotyl presents no unusual features in the region of the missing cotyledon and there are no indications of injury to the seedling.

Abnormal seedlings showing indications of schizocotyly and syncotyly are of frequent occurrence. Several stages between dicotyly and tricotyly can be distinguished, one being that in which one cotyledon is distinctly broader than the other (Fig. VIa). When this difference in size is more marked, the larger cotyledon shows two distinct apices which, however, do not always represent equal parts of the lamina (Fig. VIb): a stage approaching tricotyly can be seen in seedlings with one normal cotyledon, and one nearly twice the size, which is divided into two equal lobes for about half the length of the lamina, and possesses two midribs diverging from a

common petiole (Fig. VIc). Seedlings showing complete tricotyly possess three cotyledons which are sometimes equal, sometimes all unequal, in size (Fig. VI d,f,g,h). Three primary strands instead of the normal two are present in the upper hypocotyl of such a seedling (Fig.VIIa-f). Passing down below the collet (which occurs extremely high in the hypocotyl) these become united by central metaxylem (Fig.VII i). One strand gradually decreases in size (Fig.VII j,k), and finally disappears altogether in the lower hypocotyl, leaving the root stele exactly similar to that of a normal seedling. The same phenomenon is seen in seedlings with lobed cotyledons, but here the two traces from the double cotyledon enter in close proximity and rapidly unite to form a single strand. In connexion with abnormal seedlings of this kind COMPTON (4) suggests that "the possession of three equidistant and equal cotyledons is the culmination of a series beginning with a slightly forked cotyledon" and that schizocotyly is an "instructive parallel" in the course of evolution of dicotyly to polycotyly. If on the other hand polycotyly is primitive and dicotyly derived, as regarded by some writers, then teratological seedlings such as described above are indications of reversion to an ancestral condition.

The schizocotylous condition of these seedlings, if it be such, is possibly due to some external factor working on the very young seedling, and

causing fission in the apical region. Possibly on the other hand the embryo is tricotylous (since the hypocotyl is sometimes triarch) and the partial syncotyly may have been caused by some external factor at a very early age.

iii) Internal Morphology:

The Abnormal Cotyledon.

The anatomy of these abnormal cotyledons is interesting. Passing up from the base of the cotyledon the first change in the anatomy occurs within a very short distance of the lobes, in the central epidermal and mesophyll cells on one side of the lamina. These cells become meristematic in appearance and proceed to divide in a plane oblique to the leaf surface; the result of the division is seen in the small arch of cells which is quickly formed (Fig.VIII a). As one proceeds upwards this characteristic appearance is soon lost (Fig.VIII b), and the cells regain their normal structure. A similar activity then arises on the other epidermis and an arch of cells is again formed (Fig.VIII c). These have large nuclei and also arise by the division of a few of the epidermal and mesophyll cells. This formation occurs exactly at the point where the lobing of the cotyledons takes place. The cells between the apex of the arch and the other epidermis gradually withdraw from one another and round off, thus forming the two inner

margins of the lobes of the lamina (Fig.VIII d). The arc of meristematic cells on each margin then gradually disappears and is replaced by normal epidermal and mesophyll cells.

The general anatomy of these cotyledons is identical with that of the typical cotyledon, except in the possession of two median bundles instead of one.

The Normal Cotyledon.

The upper epidermal cells of the cotyledon are rather large and irregular in shape. In transverse section (Fig. IX) they appear approximately rectangular, measuring about 60μ in width and rather less in depth. The cells of the lower epidermis are smaller and more uniform in shape. On each surface the outer walls are slightly thickened and possess an extremely thin cuticle. Stomata are abundantly distributed over the lower, but are not found on the upper, surface. These are frequently placed also on the margins of the cotyledon where they are possibly hydathodal in character (Fig. X). The guard cells of the stoma and the adjacent epidermal cells project considerably from the level of the epidermis. All the walls of the guard cell are thickened, the inner wall (which is placed at an oblique angle due to the projection of the stoma) showing the greatest amount of thickening. The cuticle extends beyond the guard cells, thus partially closing over the stomatal pore,

and appearing in transverse section as two small projections, pointing in towards each other. The epidermal cells of both surfaces of the cotyledon occasionally contain small rounded granules, which are of a pale greenish colour and highly refringent. These granules correspond closely in appearance and reaction to those described by ZIMMERMANN (26) as 'tannin-vesicles'. They occur in all parts of the plant, both seedling and adult, sometimes very abundantly. No tannin is, however, found in the guard-cells, and it is never abundant in any parts of the cotyledon.

Multicellular hairs occur on the margins of the cotyledon in a few species (e.g. R. decorum). These arise from several epidermal cells, and have a broad base six or more cells in area. They vary in length, but are usually rather short and thick, measuring 10 -12 cells from base to tip. The hairs are of two kinds (see Fig. X). The one type bears a large club-shaped head composed of numerous polygonal cells with protoplasmic contents. These hairs are similar to those figured and described by SOLEREDER as "glandular trichomes". The nature of the secretion, if any, is difficult to determine but it is possibly mucilaginous. The other type ends in a number (usually about four) of much elongated tapering cells, which may measure more than 150μ in length, the basal cells of the hair being only about 40μ or less.

Immediately below the epidermis of the cotyledon is a layer of palisade tissue, usually one, but occasionally two cells in depth. These cells are shortly cylindrical, being often almost isodiametric in a young cotyledon. In the adult cotyledon they measure 80 - 90μ in length and about 30μ in breadth. The cells are closely packed, intercellular spaces being absent, and each contains numerous chloroplasts. This palisade tissue passes, with no very marked distinction in the average cotyledon, into the spongy mesophyll - a layer of approximately four cells in depth. The cells of this tissue are rounded, or elongated in the plane of the lamina. They contain fewer chloroplasts and are loosely arranged, with numerous intercellular spaces. The main vascular bundle is very small, and has a collateral arrangement, consisting of one or two small xylem elements (each about 10μ in diameter), and a proportionally large rounded mass of phloem. In the centre of the phloem a small cavity can occasionally be seen. This cavity is similar in appearance and position to that figured by HABERLANDT (8) as occurring in the phloem of the leaf of Aralia, and is termed by him a "secretory intercellular passage". The bundle is enclosed by a few rounded cells forming a collecting-layer, which are intermediate in size between the vascular and assimilating elements. Tannin in the form of minute granules has been found in at least

two species, occupying some of the cells of the collecting-layer, and also a few of the vascular parenchyma cells. This is rare, however, and the tannin is never abundant.

The Hypocotyl.

The leaf-trace from each cotyledon passes rapidly and directly into the main stem and the upper part of the hypocotyl therefore possesses two primary bundles. The transition to root structure is of Van Tieghem's Type 3, and takes place in the uppermost part of the hypocotyl, immediately below the insertion of the cotyledons: indeed, the change commences while the entering traces are still in an oblique position in the stem. During the transition each xylem strand (consisting of 1-3 cells) rotates on its own axis through an angle of 180°, so that the protoxylem becomes centrifugal instead of being centripetally placed (Fig.XI,XII) Simultaneously each phloem strand divides into two parts: each half passes round outside the xylem, through an angle of 90°, and unites with the half from the opposite strand. The whole of the transition is effected quickly, so that root structure obtains within 2 millimetres of the cotyledonary node. This arrangement persists for a short distance down the hypocotyl: in the lower portion of the hypocotyl the two xylem strands are united by a central development of metaxylem. The stelar arrangement, therefore, of the

lower hypocotyl is diarch and consists of a narrow plate of xylem (normally 7-8 cells in all) with a crescentic mass of phloem on each side. The phloem often shows clearly the central cavity observed in the cotyledonary phloem (Fig. XIII). The vascular system of the young seedling root is similar to that of the upper hypocotyl in having two isolated xylem strands unconnected by any metaxylem. But here the elements are fewer in number, each strand containing usually only one cell. These cells are extremely small, with thickened walls, and the two strands are separated by a small patch of thin-walled parenchymatous tissue representing a pith (Fig. XV).

The vascular strands in the hypocotyl are enclosed by a layer of parenchyma cells intermediate in size between the xylem and the cortical cells. This layer is one cell in depth outside the phloem, but at each end of the xylem plate it forms a small mass, 2-3 cells in depth. This tissue may be regarded as a pericycle. The zone of cells outside this varies in appearance according to the age of the seedling. A seedling examined two or three weeks after germination shows these cells to be exactly similar to other cortical cells; they are round in outline and often contain plastids. At the age of four to six weeks after germination the cells are still broad in shape, and all the walls stain slightly with Sudan III though not with phloroglucin. In some cases only the

tangential walls are stained. The latter probably represents Kroemer's "primary" stage (11) in endodermis formation, and the former his secondary stage. Hypocotyls of seedlings about sixteen weeks old show a double layer of cells which stain distinctly, both with Sudan III and phloroglucin. The outer layer consists of brickshaped cells, much elongated tangentially but showing very little thickening. This undoubtedly represents a "secondary" endodermis with thin walls whose whole inner surface has a suberin lamella. The inner ring of cells is very incomplete and the cells are much smaller and less uniform in size than those of the outer ring. This marks the initial stages of cork formation from a phellogen internal to the endodermis. In the hypocotyl of an eleven-months-old seedling is seen a complete band, three or four cells in depth, of thickened and flattened cork cells, immediately external to the phloem. Outside this is a completely dead and withered layer formed from the endodermal, cortical and epidermal tissues.

The cortex in the young hypocotyl (4-6 cells in depth) is composed always of large cells, 90-100μ in diameter. These are thin-walled and rounded in shape, sometimes closely packed, sometimes separated by intercellular spaces. All the cells contain numerous plastids (often chloroplasts), those nearest the centre having fewer than those towards the

external surface. Stellate crystals of calcium oxalate are occasionally found in the cortical cells. The occurrence of tannin granules in the hypocotyl is confined almost entirely to the epidermis where it occurs abundantly, but it is also found rarely in isolated cortical cells. The cells containing it are normal in structure, but are easily distinguished by the characteristic appearance of the granules, which are abundantly distributed throughout the cell. The tannin-bearing cells may occur in any part of the cortex.

The epidermis is composed of a single layer of cells, smaller than those of the cortex and polygonal or circular in outline. The outer or sometimes all the walls are slightly thickened, and the cells in nearly all species crowded with tannin granules. In very rare cases the epidermal cells exhibit a complete absence of tannin, and the presence of well-marked fine ridges on their horizontal walls, due possibly to the unequal deposition of substances on their surfaces: this has been observed only in one seedling of R.Cooperi and one of R. campanulatum (Fig. XIII). In rare cases, a large proportion of the epidermal cells are slightly papillose in structure and possess thin outer walls (Fig. XIV): these possibly function as ocelli.

The Root.

The stele of the young root is similar to that of the upper hypocotyl, the chief differences lying

in its relatively larger size, and the possession of a well-defined endodermis. In the root (Fig. XV) the phloem and stelar parenchyma are usually indistinguishable, while in the hypocotyl they are easily detected. All the conducting elements are very small, the average diameter being less than 9μ. The xylem cells have spirally thickened walls, the pith and phloem are thin-walled. The endodermal cells are fairly large, measuring 30μ or more across. They are usually square or wedge-shaped in transverse section and possess very much thickened walls, although different seedlings show a considerable variation in the extent of the thickening. A varying amount of tannin is sometimes present in the endodermis of young roots. R. decorum shows endodermal cells crowded with tannin grains, while many other species show no trace of tannin in any part of the root.

The cortex surrounding the stele is only one cell in depth in the greater part of the root. The cells composing it are large (50μ or more) and approximately square in shape. Their outer walls are always thin, but the inner and tangential walls are often markedly thickened. This phenomenon has been recorded for the roots of some members of the Ericaceae (though not Rhododendron) by VAN TIEGHEM (23). The limiting layer of the root is composed of large cells similar in appearance to, but larger than,

the cortical cells. The outer walls of these cells are always extremely thin, and this is undoubtedly correlated with the process of absorption, since the plant possesses no root-hairs. Tannin is sometimes found in the cells of the cortex and limiting layer.

Occurrence of Mycorrhiza.

Under normal conditions of growth the outermost cells of the young root enclose a dense mass of fungal hyphae, and the root thus exhibits an endotrophic mycorrhiza. The mycelium usually appears as extremely fine intracellular hyphae which are continuous with branching septate hyphae on the external surface of the root. Often it can be seen in a partially digested state (Fig. XVIc) when the hyphae are closely coiled in the centre of the cell or as a mucous, finely granular mass, which may completely fill the cell or be grouped round the enlarged cell nucleus (Fig. XVIa) The latter is apparently a further stage in the process of digestion of the mycelium by the host cells. The fungus in this state can frequently be found in masses on the external surface of seedling roots, and also within the epidermal cells of young hypocotyls. The fungus has not been found to penetrate within the stele of the root.

The mycorrhizal condition exists not only in the seedling, but in the younger portions of the adult root throughout the life of the plant. Shoot and ovary tissues in the adult plant have not been

examined for mycelial infection such as that claimed by RAYNER (18) for other members of the Ericaceae.

Lateral roots.

The lateral roots are endogenous in origin. As the young root develops, the tissues of the main root are pushed out of position, becoming compressed tangentially, until finally they are ruptured by the developing root-tip. The root-tip itself is protected by a small pad of large rounded cells forming the root-cap; this can easily be distinguished in very young stages of lateral root formation (Fig.XVII). Behind this is the mass of young tissue which forms the new root. The cells of this are large, very thin-walled and densely protoplasmic, with large prominent nuclei. They exhibit the typical meristematic appearance, being rectangular in shape and regularly arranged behind the apical meristem. Surrounding the root-tips of both lateral and main roots is a large mass of mucilage forming a broad sheath which extends some little distance behind the root apex.

The epicotyl.

Development of the plumule does not take place for a considerable period after the expansion of the cotyledons. The first foliage leaf appears seven to eight weeks after sowing, but the epicotyl may not develop further for four or five months. By this time secondary growth has united the two bundles into

a complete ring. The anatomy at a younger stage can however be seen in the elongated epicotyl of an etiolated seedling. A four months old seedling placed in the dark for a week or two shows an early stage of secondary thickening in the hypocotyl. The xylem takes the form of a solid cylinder seven to eight cells in diameter, the primary xylem being noticeable in the centre as an irregular mass. This cylinder is completely enclosed by a narrow band of secondary phloem, the two primary phloem strands being still visible as small masses within it. A short distance below the cotyledonary node, the primary xylem divides into two parts, and the central cells become thin-walled, forming a small pith. The fission of the primary phloem strands during the transition from root to stem structure can still be followed in seedlings of this age. As the cotyledonary node is approached, the pith increases in size to form a small mass of thin-walled tissue six to eight cells in diameter: these cells are considerably larger than those of the xylem. At the node itself the entry of the cotyledonary traces is usually asymmetric, one entering slightly before the other. The two traces are linked by narrow intervening arcs of secondary vascular tissue, which surround the pith and are composed of small thin-walled elements. Immediately above the node the wood cylinder is again completed across the gaps left by the outgoing traces. The

first foliage-leaf trace passes in on one side between the two primary bundles, the second a little later on the other side, and the third between the one cotyledonary trace and the first foliage leaf-trace. The phyllotaxis in Rhododendron is thus seen to be a 2/5 spiral.

The pith of the young epicotyl is rather small, and consists of a group of thin-walled cells which vary considerably in size, the largest being towards the centre. The cells are round or polygonal in shape, and are closely packed, usually without intercellular spaces. Stellate crystals of calcium oxalate are occasionally present in the larger cells and often also anthocyanin in solution. The primary xylems project slightly into the pith as small irregular masses of very thick-walled cells. The secondary wood, however, is thin-walled at this stage, the cells being rectangular in shape and irregularly arranged. (Fig.XVIII). There is an absence of medullary rays in seedlings at this age though they develop later. A layer of cambium separates the xylem from the secondary phloem, of which there is very little. The phloem cells are small, thin-walled and irregular in shape, with large nuclei.

The cortex is not uniform in character, but has a broad central portion differing in texture from the outer and inner layers. The inner layer, adjoining the stele, consists of about three rows of small cells,

the innermost ones being the smallest. These cells are round and thin-walled, and often possess large nuclei. The differentiation into two distinct types of cell, which is a characteristic feature in the central cortex of adult plants, is here beginning to develop, and is indicated at this stage mainly by a variation in size of the cells. The larger cells measure sometimes as much as 90-100μ, while the small ones may attain only 35μ in diameter. The latter form an irregular network in which the former are situated. Both are thin-walled with large nuclei. Large stellate crystals of calcium oxalate are extremely common in the large cells, while anthocyanin in solution occurs in the small-celled tissue. These crystals are abundantly distributed in the neighbourhood of a bud- or leaf-trace: this is a noticeable feature also at the node of the adult plant. The outer cortex consists of a layer, one to three cells in depth, of small cells similar to those of the inner cortex. This is bounded by an epidermis of medium-sized polygonal cells with thin or slightly thickened walls. The outer walls are sometimes thinly cutinised. Stomata occur infrequently on the epidermis of young epicotyls. These are identical in structure with those found in the cotyledon, but do not usually project from the level of the epidermis.

At least four types of hair are found on the young epicotyls of Rhododendron. Of these, three are multicellular, one unicellular. The latter is a

slender colourless hair arising from one epidermal cell, and measuring as much as 300-400μ in length (Fig.XIX d). It occurs in many species, including R. calostrotum and R. praevernum. Two of the three multicellular types are similar to those found in the cotyledon, but are larger and may be more complicated in structure. The capitate type already described is fairly frequent on epicotyls of R. decorum, R. campylocarpum, R. praevernum, etc. The head often contains anthocyanin, and probably other substances also whose nature is difficult to determine. The third type also is similar to some of the cotyledonary hairs but here the stalk cells are sometimes much more irregular in shape and the tapering apical cells more numerous, much longer and more varied in length. These tapering cells are thin-walled and without living contents. They are usually light brown in colour and may reach nearly one millimetre in length. The fourth type of hair is described by SOLEREDER as a "peltate gland", and may be of considerable size. The young epicotyl of R. Cooperi is densely clothed with these scaly hairs, one of which may surround as much as a third of the whole circumference of the epicotyl (Fig. V). The hair consists of a short thick multicellular stalk, and a large expanded disc-like head. The centre of the disc consists of a convex mass of polygonal cells, from which radiate out numerous much elongated cells, arranged to form an annular membrane round the central mass. The

relative sizes of the central and peripheral portions vary greatly in different species: this can be seen from Figs.XXXIIIa,c,XXXIV.

These hairs are apparently of a glandular nature and are cited by DE BARY (5) as examples of "intramural" secretion. He states that the secretion process occurs between the longitudinal cell-walls, which in their central portions become isolated from one another (Fig.XXXIVb), the interstices being filled with the secretory mixture of resin and ethereal oil. VESQUE classifies these peltate hairs as 1) those which remain glandular, e.g. R. Maddenii, R. ferrugineum and others, 2) those which are purely membranous e.g. R. argenteum and R. arboreum. It seems however that those of R. argenteum and R. arboreum are of a different type from the peltate ones now under consideration, and these are described in a later section (p.56). The peltate hairs are, in some species at least, undoubtedly glandular when young, containing abundance of oil: their contents are however soon lost, and the adult hair in all species seems to be purely membranous.

C. THE YEAR-OLD SEEDLING.

i) External Morphology.

Seedlings of Rhododendron after a year's growth vary greatly in appearance and size. Some species

are slender and may attain a height of eighteen centimetres or more (e.g. R. triflorum, R. lepidotum), while others remain very short, often measuring less than a centimetre above ground level (e.g. R.hirsutum and others). The leaves of short seedlings are usually dark green, comparatively large, and leathery in texture, as in R. decorum and R. campanulatum. R. decorum at the age of twelve months possesses six to ten leaves, the largest of which do not attain more than a quarter of the normal adult size. R. lepidotum on the other hand when only seven months old may possess over fifty leaves, the great majority of which have reached full adult size.

The leaves of the seedlings show all the variations in colour, shape, etc. seen in the adult leaf. The colour and texture may be dark and leathery as in R. decorum, or light and delicate with sometimes a waxy surface, as in R. triflorum and R. polylepis. Peltate scales, white or brown in colour, are extremely numerous in certain species and occur on both surfaces. White hairs, which may be long and tapering as in R. Veitchianum, or short and thick (R. arboreum), sometimes form a close fringe on the leaf edges. In some cases these hairs are abundantly distributed over the whole upper surface, as in R. villosum where they stand erect, and in R. Mariesii in which they lie appressed on the surface, pointing towards the apex. Another type of hair is commonly found on both surfaces of the young leaves. This is brownish in

colour and repeatedly branched, each hair thus forming a small tuft arising from a multicellular stalk. These hairs give the appearance of a thin fluff which is easily rubbed off, and is most abundant on the plumule and undeveloped leaves.

Anthocyanin occurs in the shoot tissues of the seedling in many species. The plumule and youngest leaves often have a pink colouration which may fade as development proceeds. Often the entire epicotyl, and sometimes the leaf bases, show the presence of anthocyanin; but it is most frequently found in the spongy mesophyll of the leaf imparting a vivid red colour to the under surfaces.

Type Seedling.

A seedling of Rhododendron decorum at the age of twelve months stands about two centimetres above the ground, the epicotyl and hypocotyl being approximately the same length. The plumule and leaves (of which there are about six) are hairy on all surfaces. These hairs are similar to those present in the cotyledon. The first three or four leaves are shortly petiolate, and measure only half a centimetre or so in length, those which follow being more than twice this size. The cotyledons sometimes persist in a withered condition on the hypocotyl. The epicotyl is green, hairy and rather thick, while the hypocotyl is always glabrous, woody and brown, and usually more slender. The root system is large, consisting of a long main root which may reach a length of more than fifteen

centimetres. From this numerous fine lateral roots arise at intervals along the main axis.

ii) Internal Morphology.

The Leaf.

The leaf of Rhododendron decorum at twelve months presents no unusual anatomical features. The midrib is prominent on the basal portion of the leaf, projecting out considerably on the under surface (Fig. XX). The vascular bundle throughout the petiole and lower lamina is collateral in arrangement and of a roughly semicircular shape, becoming much smaller and more rounded as it ascends. This arched form is the consequence of slight secondary growth which arises from a cambium within the bundle. The secondary wood is laid down in rows of about six cells in depth, which are traversed at frequent intervals by medullary rays whose cells are crowded with food reserve. Outside this is a narrow zone of small phloem cells. The primary xylem, with a little parenchyma, is situated on the inner side of the arch, and the bundle is strengthened on its under and upper sides by a mass of thick-walled mechanical tissue. The elongated palisade cells of the leaf give way to smaller, rounded and often tannin-bearing cells immediately above the vascular bundles. The palisade mesophyll itself forms two layers below the upper epidermis but the layers are not uniform in appearance.

The cells of the upper layer are cylindrical, regular in shape and closely packed together. All are crowded with chloroplasts. The cells below this are more loosely arranged, broader and more rounded in shape, and contain fewer chloroplasts. This layer is most apparent above the main vascular bundle of the leaf, and there may be a third irregular layer of rather rounded palisade cells below the second, but this tapers out towards the margins of the leaf. The spongy mesophyll is composed of rather large irregular-shaped cells forming a loose tissue three to four cells in depth. Occasional stellate crystals of calcium oxalate are found in its cells. The upper epidermal cells are large, rounded and regular in shape: those of the lower are smaller and less regular, and their continuity is broken at intervals by stomata. These project slightly from the surface and are exactly similar in appearance and structure to those described in the cotyledon. The epidermal cells on both surfaces of the leaf have their outer walls moderately thickened. Hairs of several types already described are found, arising from upper and under epidermal cells, in R. decorum and other species. These give rise to the various forms of indumentum found in the adult leaf.

Tannin is abundant in the neighbourhood of the midrib in the lower lamina and petiole. It occurs as large granules in all the tissues except the xylem,

and can sometimes be seen forming a thin coating round the chloroplasts of the mesophyll tissue. It is most abundant in the medullary rays, the spongy mesophyll and the epidermal cells, and occurs in smaller quantity in the phloem and palisade tissue. Tannin is absent in the upper part of the lamina.

Epicotyl.

The epicotyl of a twelve-months-old seedling measures three or four times the diameter of the young seedling epicotyl, but the anatomy is very similar. This increase in girth is due to secondary growth in the stele, and also to expansion of the pith by increase in size of the cells and by development of new cells: this latter now occupies nearly one half of the total diameter. The pith and cortex show clearly the differentiation into two kinds of cell which was beginning to develop in the younger epicotyl. The smaller cells of both pith and cortex are rounded, and possess slightly thickened walls and numerous chloroplasts. The large cells are irregular in shape and thin-walled, with no contents except occasional large crystals of calcium oxalate. Immediately below the epidermis the small cells form a complete layer one or two cells deep, the walls of which exhibit greater thickening than those in any other part, thus affording partial support to the stem. The epidermal cells are oblong in shape, with thickened walls and abundant tannin granules. Stomata are occasionally found projecting from the level of the epidermis. Unicellular

and multicellular hairs arise from some of the epidermal cells, occurring most abundantly near the shoot apex. Tannin is present in all the tissues at the youngest portion of the epicotyl, but gradually disappears in the basal part of the stem. This is the case also in the adult plant where the apical portion of the stem contains a considerable amount of tannin in its tissues, while the greater part of the stem shows a complete absence of it. In the epicotyl, as in the leaf, it occurs either as large granules, or as a thin film round the chloroplasts or protoplasm of the cell. It is seen in the latter form in the medullary ray cells and in the phloem.

The secondary wood at this age has increased to a depth of eight or nine cells whose walls are now markedly thickened. The cambium layer separating it from the phloem is easily visible.

The hypocotyl.

The hypocotyl at twelve months (Fig.XXI) differs considerably in its anatomy from that of a young seedling. This is due to the activity of wood cambium and phellogen producing a large mass of secondary vascular and cork tissue. Approximately seven-tenths of the diameter is now occupied by the wood tissue. In the centre the plate of small-celled primary xylem can be seen: this is surrounded by a considerable thickness of secondary xylem whose elements are mostly pitted tracheids, radially arranged. These rows of secondary wood cells are separated by numerous medullary rays

whose cells are rounded in shape and contain abundant food material. These rays are mainly uniseriate but may be sometimes two to three cells wide, and they arise in all parts of the wood. Some extend the whole way from the primary xylem to the phloem, others only through the inner or outer part of the wood. A large proportion of the tracheids also, especially the outermost ones, contain food material so that the medullary rays are connected tangentially by rows of food storing cells. The food reserve thus stored is starch which is present in great abundance. The grains are rounded and very large, one sometimes completely filling a cell.

The phloem, which forms a narrow layer 4-5 cells in depth, is separated from the secondary xylem by a layer of typical cambium cells. The phloem cells are large and possess rather thick walls. All contain abundant food reserve and many possess large nuclei. The cork cambium, being of pericyclic origin, arises immediately outside the phloem, and at this stage two or three rows of cork have been formed. The cork cells are large, thin-walled and tangentially compressed. They contain a deeply-staining granular substance which is probably tannin. The cortex, which occupied a large area in the hypocotyl of the young seedling, has been cut off by this cork layer and appears as a withered, compressed band of dead tissue; this, together with the dead epidermis, forms a thin bark which is readily exfoliated.

The root.

The upper part of the root in a year-old seedling is identical in its anatomy with the hypocotyl. In the lower portion where there is little or no development of secondary wood and no cork cambium, the root closely resembles the young seedling root described above. The only difference lies in the stele, the primary xylem strands being here united by an irregular central development of metaxylem whose cells are large and thick-walled. The small delicate phloem cells become crushed by this addition of wood, and individually are not easily distinguishable. A thin-walled pericycle, one cell in depth, lies between this and the endodermis. The remaining tissues present an appearance similar to that of the young seedling. The endodermis is prominent, with markedly thickened walls, the thickening extending up the radial walls of the cortex also. The cell-walls of the limiting layer also are thickened, but these cells appear to be easily worn off during growth. These, and sometimes the cortical cells, contain fine threads of the mycorrhizal fungus.

D. DISCUSSION.

The chief point which arises from the examination of the seedling anatomy of Rhododendron is its extreme uniformity. Even if one takes into account the

probable influence of a uniform environment in early life, this marked structural uniformity of the seedling is rather surprising in an Order which exhibits a considerable range of habit and in which progressive tendencies are still actively at work: and not less surprising when the variation in seed characters (size etc.) is recalled. Much work has been done on the variation in seedling structure within genera and species, and on its relation, if any, to the habit of the mature plant. In this connexion the work of LEE (12) on the Compositae, and of COMPTON (3) on the Leguminosae, is interesting. LEE found that not only seedlings of closely related species, but different seedlings of the same species showed diversity in vascular structure. Variation within species which are comparatively new and fluctuating and which present such wide diversity of habit and form as do some of the Compositae, is more comprehensible than if they were exhibited in a comparatively conservative genus like Rhododendron. The conclusion reached by her, however, is that of several other workers on seedlings, viz., that it is not possible to use seedling anatomical features as indications of affinity.

COMPTON's conclusions for the Leguminosae were, briefly:

1) production of large seeds and seedlings is correlated with the tree-habit.

Vascular structure in a seedling stands in intimate

relationship with physiological needs, so that
2) Large seedlings show tetrarch symmetry, and
3) Reduction in size of the seedling gives eventually a diarch symmetry, and once attained, this is extremely stable; therefore,
4) tetrarchy being associated with the more primitive (arborescent) habit, it is a fundamental condition, and diarchy derived.
5) The diameter of the seedling axis determines the level of the transition, a high transition being characteristic of slender seedlings.

Although it is unwise to apply generalisations of this kind on one group of plants to a different one, yet a comparison between the two is admissible. The results of the present anatomical investigation are at variance with COMPTON's first point, but in agreement with most of his later ones. There appears to be no relation between size of seed and adult form in Rhododendron (as studied from 50 species). One has but to compare the seed of R. arboreum or R. maximum (the mature forms of which are both arborescent), with that of R. ferrugineum or R. hirsutum (both alpine shrubs), to see that this is the case. However, all the seedlings of Rhododendron examined during the work were exceedingly small and showed diarch symmetry (which is apparently a very stable condition) and an extremely high transition-level. Since the section on seed and seedling anatomy was completed, one species

(R. quinquefolium) has been found which produces an extremely large seedling (in proportion to the normal), the cotyledons measuring nearly one centimetre in length instead of the typical 2-3 millimetres. The seed of this species is not unusually large, but was found to produce seedlings with tetrarch symmetry. This condition is made the more interesting by the fact that R. quinquefolium is a small low-growing form belonging to a series which is relatively new (as indicated by its meristic precision and small habit), and in which at least seven of its members (R. Vaseyi, R. arborescens, R. japonicum, R. serpyllifolium, R. Tschonoskii, R. reticulatum, R. Schlippenbachii) possess the normal diarch symmetry.

Even if one explains the tetrarch condition as being correlated with the large size of the seedling, one is prevented from suggesting a reduction tendency in size and symmetry of seedling in Rhododendron by the high position of this particular seedling in the genus. Further, without additional examples of tetrarchy, it is not legitimate to draw conclusions from this apparently anomalous case. One can however state that, within the species studied, no indications of the specific characters found in the mature plant are exhibited by the seedling.

III. THE ADULT PLANT.

III. THE ADULT PLANT

A. THE ROOT AND STEM.

i) External Morphology.

The root.

The root system of an adult plant is not very large, but consists usually of a main axis which rapidly tapers, and almost equally developed lateral axes, all of which bear masses of extremely fine fibrous roots, so that a closely matted system is formed which does not penetrate very deeply into the soil.

The stem.

The adult stems of different species naturally show many variations but the main features are common to all. The stem is cylindrical and the leaf-bases rather prominent. The production of bark occurs early, often in the current year's growth, and the junction of the bark and green tissue is sometimes extremely irregular. (For details of this see Section IV, p.78, and Fig.LVII). The bark varies in character, in R. decorum and others being rather rough in texture. In other species it may be either very smooth and papery and of a bright reddish colour, (e.g. R. Falconeri, R. sino-Nuttallii) or rather furrowed as in R. himalaicum. The lenticels are always very small and roughly circular in shape. Another feature observed in nearly all species is the relatively rapid

growth of the lower portion of each year's shoot, so that the foliage of successive seasons becomes separated by long naked internodes, the nodes being represented by the bud-scale scars. The upper portion sometimes develops very little, and the result is a dense terminal rosette of spirally-arranged foliage leaves. When the branches arising in the axils of these leaves are developed, a true whorled arrangement is simulated. This is not so easily seen in R.decorum as in smaller forms such as R. hypolepidotum where the apical bud is a flower bud, and the lateral branches develop more or less equally around it. In R. decorum the green stem is smooth except for the presence of a few very fine short hairs. In others it may be downy (R. floribundum), waxy (R. Griffithianum), or thickly clothed with hairs. In R. crassum and many other species the hairs are all peltate, in R. Griersonianum noticeably glandular, while in a number of small forms (e.g. R. yedoense) long brown appressed hairs clothe the stem, with their apices directed upwards. An extremely thick white or brown felt is found on the young stems of a great many species.

ii) Internal Morphology.

The root.

The root of the adult plant resembles closely in its anatomy that of the year-old seedling, and differs

only in its larger size, due to more advanced secondary growth of vascular tissue and additional development of cork tissue.

The stem.

The adult stem of R. decorum presents some marked differences from the stem of a year-old plant. The pith (Fig.XXIIb) conforms with that described by GRIS as a "heterogeneous pith", frequently met with in Dicotyledonous ligneous plants. The great majority of the cells have lignified walls and are small and much pitted. They contain plastids (often chloroplasts) and abundant starch grains. These are the "cellules actives" of Gris. In this tissue are embedded small groups of large, very fine-walled cells ("cellules inertes") with no contents except numerous stellate crystals of calcium oxalate. These groups are composed of three to five cells, from which large cavities often arise lysigenously: these are usually completely occupied by the crystals.

The pith of R. longistylum (a small form having a homogeneous pith), shows an interesting feature which has not been observed elsewhere. The pith cells are approximately uniform in size and thickness of wall, except at the base of the apical bud. In this region a large number of the cells possess extremely thickened walls and have the typical appearance of sclereids (Fig.XXXIII). These sclereids can be found at the base of each year's growth (in the position of

a former apical bud), and immediately below it, but they are quickly replaced by normal pith cells in the remainder of the stem.

The cortex of R. decorum shows the same differentiation in its tissue as the pith, but here the thin-walled masses are often much larger, especially in the central and inner parts (Fig.XXIIa). The crystals however are not nearly so numerous in the central cortex and are usually smaller. They occur in great abundance immediately outside the fibrous layer of the pericycle, and in the thin-walled groups of tissue near the epidermis. The crystals are also extremely numerous in pith and cortex in the region of a leaf- or bud-trace. The outer cortex, five or six cells in depth, possesses thicker cell-walls than elsewhere, and encloses no thin-walled tissue. All the small cortical cells contain chloroplasts, the outer region possessing them most abundantly. The epidermal cells rather small and square in shape, with thickened walls which are usually heavily cutinised on their outer surface.

It is interesting to find that this differentiation of tissue is not seen in all species of Rhododendron, but seems to be confined almost entirely to the large-leaved forms such as R. decorum, R. auriculatum, R. Hodgsonii etc. The very small-leaved forms have a uniform pith and cortex, both of which are relatively small, e.g. R. telmateum, R. serpyllifolium (Fig.XXIV), R. hippophaeoides and R. austrinum. There are,

however, many species with rather small or medium-sized leaves, which show a slight or distinct differentiation into the two kinds of tissue in their cortex, the pith remaining uniform throughout, or practically so. The following are examples of this: R. leptothrium, R. ledifolium, R. bracteatum, R. racemosum and R. primulinum (Fig.XXV). In these the pith cells are all thick-walled, and vary a little in size, the larger ones containing single crystals of calcium oxalate.

In connection with this differentiation of tissue two series of Rhododendron appear to be exceptions. 1) Many, if not the majority, of the members of the series Maddenii possess distinctly large leaves, the lamina reaching a length of eighteen to twenty-three centimetres in R. crassum, R. Nuttallii, R. megacalyx and others. They all, however, possess a pith which is uniform in structure, or in a few cases shows a very slight differentiation in its cells. It will be seen later that this series shows "small-leaved" characteristics in its nodal anatomy also. The second series is an exception in the opposite direction. The members of the series Thomsonii are nearly all small-leaved, as the following list shows:

Species	Average length of lamina
Thomsonii	6 - 7 cm.
callimorphum	5 - 6 cm.
cyanocarpum	8 - 9 cm.
Meddianum	8 -10 cm.
Wardii	10 cm.
rhaibocarpum	6 - 7 cm.

All of these, however, show a definite and often marked differentiation of pith and cortex. It will be seen that this series exhibits "large-leaved" characteristics also in its nodal anatomy, showing five vascular strands on the leaf scar.

The rest of the stem anatomy presents no unusual features. Annual rings are discernible and often sharply defined in the secondary wood of an old stem. The spring wood contains many large vessels, polygonal in shape and with slightly thickened walls, while in the autumn wood the vessels are small and square, with small lumina and highly lignified walls. The rows of secondary xylem are traversed at frequent intervals by medullary rays, usually uniseriate but sometimes multiseriate. These rays extend from pith to phloem, and contain abundance of starch.

Mechanical support is given to the stem in two ways. In many species sclereids are abundantly distributed throughout the cortex (e.g. in the young stem of R. primulinum, Fig.XXV). These occur singly or in groups, and are extremely large, thickwalled, and irregularly polygonal in shape. They develop as the result of sclerosis of a few of the large thin-walled cells, and are not present in the small-celled tissue of the cortex.

The other mode of support is found in every species of Rhododendron examined. Immediately outside the secondary phloem in an adult stem is a layer, three or four cells in depth, of fibrous cells which

are small and usually extremely thick-walled. This layer may be continuous round the stele, but is usually broken up into groups of cells, the gaps between them being often radially continuous with some of the larger medullary rays which penetrate through the phloem. That these fibres are pericyclic in origin is apparent partly from their position, but chiefly from the fact that endodermal cells are sometimes found separating the fibres from the cortex. These endodermal cells are recognisable by their thinly suberised walls, and are found only in the small heath-like forms of the genus. In these (e.g. R. complexum, R. impeditum, R. orthocladum, R. hippophaeoides) an almost complete endodermis is present in the young adult stem.

The cork cambium is in all cases pericyclic, originating between the phloem and the pericyclic fibres. Its development, together with that of the later cortical cambium, is described in another section (p.72).

B. NODAL ANATOMY.

The phyllotaxis in Rhododendron is a 2/5 spiral. The leaves possess a short stout petiole and a swollen base, which is broad and leaves a triangular or crescentic scar. The vascular supply of the petiole, seen in the transverse section, has an inverted triangular or elliptical form, the upper central portion of which is discontinuous, in the basal part of the petiole. This strand enters the stem in one of two ways: it may pass in through the leaf-base as a single trace, forming a crescentic projection from the main wood cylinder for some distance down the stem. This type of leaf-trace is found in the majority of species with small or medium-sized leaves, e.g. R. moupinense, R. yanthinum, R. irroratum. The other method of entry is seen in the large-leaved forms such as R. Hodgsonii, R. decorum, R. argenteum, R. floribundum. In these the trace divides into several smaller strands which branch out in the leaf-base, thus affording the leaf better mechanical support. The number of traces in the leaf-base is usually five, or less frequently seven, but fusion or further division of the small strands may cause many variations in the leaf scar, even on one stem (e.g. R. giganteum, R. Nuttallii, R. auriculatum). The arrangement also of these strands on the scar varies within the same plant, but in the great majority of species they exhibit a U-shaped formation in the centre of the scar.

Where there are seven strands, five are grouped round the centre and one placed at each upper corner of the scar.

The mode of union of the foliar traces with the main vascular supply of the stem varies according to the arrangement of the strands in the leaf base. The principle is however the same in each and can be followed in R. floribundum. This species shows five distinct strands on the leaf scar. These are formed by the fission of the petiolar trace into one median and two pairs of upper lateral strands. These strands are concentric in arrangement but become collateral as they enter the stem. Each is surrounded by a zone of fibres which enter with the strand, thus completing the ring of pericyclic fibres below the node. The method of fusion of the strands with the main stele depends on the direction (downward, upward or outward) which the strands take as they pass through the cortex. Figs XXVI, XXVII illustrate this. Perhaps the most frequent method is that shown in Fig. XXVIa where the three lower strands fuse while passing obliquely downwards through the cortex, the two upper passing more or less directly in and uniting with the stele immediately below the bud trace. This upper pair may however turn upwards and join the bud trace almost immediately. When the leaf-base possesses seven traces the two extra ones either pass almost directly inwards and downwards, (sometimes fusing with the three lower strands, sometimes remaining free,

Fig.XXVI(b,d); or, more frequently, they take an outward and sometimes downward course, to join the stele at points between this and the next leaf-trace. Fig.XXVIII represents, diagrammatically, tangential longitudinal sections showing the traces as they enter from the leaf-base to the main stele. The gap left in the main cylinder between the bud- and leaf-traces is sometimes, if not always, closed up, and may continue so for some distance. It is probable that this gap may be open in young stems and that it becomes closed over by a later development of vascular tissue as the stem and leaf mature.

It is on account of this rather irregular fission of the leaf-trace in the large-leaved species that the number of bundles in the stem is difficult to determine. In small forms of Rhododendron five primary bundles are visible, entering as single traces from the leaf-base.

The series Maddenii and Thomsonii are exceptions to the general rule of "large-leaved" and "small-leaved" types of leaf-trace. The average leaf of the Maddenii group is distinctly large, but all have single leaf-traces passing through the leaf-base as one strand. The leaves of the Thomsonii series on the other hand are definitely small, being short, rounded and very broad; but all show five separate strands in the leaf-base entering the cortex to unite with the main stele in the way already described for R. floribundum.

C. THE LEAF.

i) External Morphology.

A large number of Rhododendrons are deciduous, but the great majority of species are evergreen, retaining their leaves for two or three years or more. The deciduous species are all shrubby forms possessing small, light green leaves which are delicate in texture. All the leaves possess short petioles, which in a few species curve over so that the lamina is directed downwards, giving a drooping appearance to the plant. Many leaves are slightly revolute at the margin, and leaf-rolling, consequent on loss of water, is a characteristic feature. The size of the leaf varies between 60 cm. in length by 20 cm. in breadth (as in a mature leaf of R. grande), and 6 mm. by 3-4 mm. in R. serpyllifolium. The leaves fall roughly into three groups according to their shape: 1) those which are long, narrow and very pointed, e.g. R. ovatum, R. argenteum, 2) those which are broad and very rounded at the apex, in some cases being nearly as broad as long, e.g. R. Thomsonii, R. fulgeus, R. decorum, 3) an intermediate type with a broad lamina and pointed apex, e.g. R. grande, R. Nuttallii, R. crassum.

The colour varies from a dark green in leathery leaves such as R. Hodgsonii and R. Kingianum, to a light sometimes yellowish green in R. Nuttallii,

R. sulfureum and many of the deciduous forms. A vivid red colour, due to abundant anthocyanin in the tissues, is often present in the very young leaves of many species (e.g. R. Boothii, R. nematocalyx). Sometimes the pigment is confined to the peltate scales which form a complete covering on the young leaves of such species as R. Nuttallii and others. This pigmentation quickly disappears on development of the leaf. Anthocyanin is distributed also throughout the mesophyll tissue of adult leaves in many species, giving them a deep red colouration on the upper or under surface according to its localised distribution in the palisade or spongy mesophyll.

The leaf surface is sometimes very smooth, due to a well-developed cuticle, or covered with a bluish wax as in R. cyanocarpum and R. Thomsonii, but in the majority of species is pubescent. The hairs can be classified under three heads by their general appearance: a) fine unbranched hairs, e.g. those found in R. Weyrichii, R. yedoense, b) branching hairs, often of a vivid red or broad colour, and forming a thick fluffy indumentum on the lower, and sometimes upper, surface of the leaf, e.g. R. Falconeri, R. aemulorum, R. pendulum, c) peltate scaly hairs, found in R. Maddenii, R. camelliaeflorum, R. bracteatum and many others. This last type gives a characteristic "granular" appearance to the leaf surface. The scales are extremely numerous, measure somewhat less than half a millimetre in diameter, and occur on all parts

of the plant. They are usually of a transparent white colour on their first appearance but become light brown as the leaf matures. The unbranched hairs occur on both surfaces and on the margins and petioles of many leaves. They measure two or three millimetres in length, and usually lie appressed on the lamina, the free end directed towards the leaf apex. Erect, stiff hairs, also unbranched, with viscous club-shaped heads, occur on the petioles in many species, e.g. R. habrotrichum. These hairs are often deeply coloured with anthocyanin, and measure sometimes more than a centimetre in length.

ii) Internal Morphology.

Cuticle.

On the upper surface of the leaf the cuticle is well-marked and sometimes very thick (e.g. R. anthropogon, R. pendulum). It is usually smooth, but occasionally roughened on its outer surface (Fig.LIII). On the lower surface the cuticle is usually very thin, especially in the small-leaved forms such as R. bracteatum and R. primulinum. Over the guard-cells of the stomata it is thickened to form a projection which partly closes the stomatal pore. In transverse section this thickening appears as two small projections which vary considerably in size and thickness in different species (cf. Figs.XL a,b,c,d.)

Hairs.

Various types of hair arise from the epidermal

cells, the majority being confined to the under surfaces. Structurally they can be classified under three heads: a) the multiseriate unbranched type, b) the multiseriate branched type, and c) the peltate type. More than one type of hair may occur on the same plant. Various forms of the multiseriate unbranched type are found. Fig.XXIXa shows a form similar to that seen in the cotyledon of R. decorum, but here it occurs on the upper surface of many leaves. A group of epidermal cells gives rise to a short multiseriate stalk; to this are attached long, rather tapering cells which adhere closely to one another. This form of hair is rare, but may be seen on the upper surface of the leaf of R. pendulum. Another form, also similar to that found on cotyledons of R. decorum, is the short thick multicellular hair with a ellipsoidal head, whose cells are very small and either densely protoplasmic or possibly mucilaginous. This hair is of a dark brown colour and occurs on the under surfaces of leaves of R. decorum, and on both surfaces in R. obtusum and other species (Fig. XXIXb). Extremely long wiry hairs, such as those in R. bullatum (Fig.XXXa) form a very thick indumentum on the under surface in this and other species. These hairs are multiseriate at their point of attachment, and taper very gradually, becoming uniseriate at their apex. The cells are thick-walled and extremely elongated, usually projecting a little at their junction with the adjoining cell. Fig.XXXc shows a

type of hair found frequently on leaf margins, and occasionally on the upper surfaces of the leaf. The hair is rigid and pointed, composed of much elongated cells whose ends project out from the axis to a greater extent than in the previous type. The cells frequently contain small rounded bodies which are probably of a secretory nature. The hairs represented in Fig.XXXb and XXXd are exclusively petiolar structures. They vary greatly in length and possess a viscous club-shaped head which is deep red in colour. The head secretes a gummy substance which swells considerably in water. In these hairs the cells are not elongated, but remain approximately the same size as the epidermal cells.

The multiseriate branched group of hairs differ greatly in structure from the preceding group. Fig. XXXI shows three forms with similar construction. Fig.XXXIb is a very frequent type of hair, colourless or light brown, which can be seen on the leaf surfaces of R. schistocalyx, R. galactinum, R. prophantum, R. floribundum, etc. The main axis is multiseriate and bears a number of branches which are divided from it by septa. These branches are sometimes unicellular (Fig.XXXIc), but in the more complex forms are sparingly septate (Fig.XXXIb). In R. aemulorum and R. Griersonianum the hair possesses a long multicellular and multiseriate stalk bearing a thick tuft of fine septate branches all of which arise approximately at the same level. A third type is found

forming small isolated brown tufts which are confined to the veins on the under surface of leaves of R. Hookeri, etc. (Fig.XXXIa). Here the axis of the hair is short and very broad, and bears a thick mass of septate branches arising at all points from it. The cells are often crowded with small bodies similar to those seen in the hair of R. austrinum (Fig.XXXc). A different type of branched hair occurs in R. fictolacteum, R. Hodgsonii, R. Falconeri, etc. Here the hair is either funnel-shaped (Fig.XXXIIa) or saucer-shaped with a rather slender stalk (Fig.XXXIIb). The whole is composed of large, irregularly polygonal cells which are rather thick-walled and form a web of tissue completely covering the under surface of the leaf. On the free edges of the hair some of the cells elongate to form uniseriate chains. These chains are, as recorded by JESSON (9) unicellular in some species (e.g. R. Hodgsonii) and multicellular in others (e.g. R. Falconeri).

The peltate type. By far the commonest form of peltate hair is that found in R. camelliaeflorum (Fig. XXXIIIa) and many others. This consists of a very short multiseriate stalk bearing a disc-shaped head. The disc consists of a central mass of polygonal cells, and an annular rim of very much elongated thin-walled cells radiating out from it. These scale-like hairs are colourless and silvery on their first appearance, but soon become a bright brown in colour. When young the cells, in some species at least, contain abundant

oil droplets (Fig.XXXIV a) and probably other contents also, but in most species, if not all, this rapidly disappears, leaving the scale empty and membranous. The relative sizes of the central umbo and the outer rim of cells vary in different species. In R. camelliaeflorum the radiating outer cells are very long, while in others e.g. R. hirsutum (Fig.XXXIV) the central mass is very large and prominent and the outer rim extremely narrow. This excessive development of the central portion gives the hair a highly convex surface. A similar type of hair, found in R. anthopogon and R. ledoides, can be seen in all stages of development on the under surface of the leaf. Fig.XXXV shows four stages in the growth of the hair from the rounded shortly stalked head to the long-stalked expanded disc form which the hair eventually assumes. The long stalk and the irregular outline of the disc, due to unequal elongation of the ray cells (Fig.XXXIIId) differentiate this hair from the preceding type. Another type of peltate hair is found in R. pendulum (Fig.XXXVI) and described by BREITFELD as a cup-shaped formation due to the upward, instead of outward, direction of the ray cells around the central disc. A careful examination of this hair however leads one to regard it as a solid mass of elongated cells representing only the central disc of a normal peltate hair, the ray cells being absent.

VESQUE distinguishes two kinds of peltate hairs

- those which remain glandular, and those which are purely membranous and not secretory. It seems however that at least the common form of peltate hair (seen in Fig.XXXIIIa,c) secretes a considerable amount of oil when young, but at maturity is completely devoid of contents. DE BARY describes this type of hair in Rhododendron as an example of "intramural" secretion, the interstices between walls containing the secretory product (Fig.XXXIVb). As an example of the purely membranous type VESQUE cites the hairs of R. arboreum (Fig.XXXIIIe): here the central mass is usually represented by two, or rarely four, rounded cells with much thickened walls. The ray cells project irregularly out from this centre, and are apparently free from one another or at least partially so, and in many cases overlapping. These hairs are small, very delicate, and devoid of contents in all stages of development. They form a dense white indumentum on the under surfaces of leaves of R. arboreum and R. argenteum. A similar hair with numerous very fine filaments radiating from a short central stalk forms the vivid brown felt on the leaves of R. fulvum (Fig. XXXIIIf).

Various classifications and evolutionary trends have been suggested by different writers for the hairs described above. SOLEREDER places the hairs of the Ericaceae in three groups: a) clothing hairs (excluding the peltate type), b) glandular hairs e.g.

R. lanatum (also excluding the peltate type),
c) Peltate hairs, being both clothing and glandular. The glandular hairs described by him as occurring in R. lanatum have not been found in that species during the present study, but are probably of the same type as those of R. obtusum (Fig XXIX b). Twin hairs as figured by him have not been seen. VESQUE also suggests three groups for the Order, namely: (1) protective unicellular, 2) protective multiseriate, and 3) glandular. BREITFELD traces a sequence in Rhododendron from an ellipsoidal long-stalked "lanatum" type to the cup-shaped "pendulum" type, thence to the types of R. Dalhousiae, R. anthopogon and R. caucasicum respectively: with the isolation of the ray cells and the reduction of the central disc he reaches the "arboreum" type of hair and thence to the large tufted "grande" form. His sequence however appears strained and the hairs of R. Dalhousiae and R. grande are inaccurately figured by him, the scale of the former species being in reality identical with his "caucasicum" type.

JESSON also suggests a sequence from the simple peltate scale to the "cup-shaped" hair of R. anthopogon with its long stalk; thence to that of R. Hodgsonii by excessive development of the central disc, and finally to the complex funnel-shaped hair of R. Falconeri. If, however, one regards the hair of R. anthopogon as a solid mass without ray cells it might well be a simpler, rather than a more advanced,

form of the normal peltate hair: moreover, the correlation, without intermediate stages, of the large hollow "Hodgsonii" or "Falconeri" type, with its irregular web-like structure, and the typical peltate scale of R. Maddenii and others, seems hardly justified.

A sequence may be tentatively suggested from the ellipsoidal type of hair (Fig.XXIXb) through the "pendulum" and "camelliaeflorum" types respectively (Figs.XXXVI &XXXIIIa), until the "anthopogon" type is reached. Another group also showing possible affinities might be one linking the hairs of R. aemulorum (Fig.XXXIc) and R. Hookeri (Fig.XXXIa) with R. Hodgsonii (Fig.XXXIIb) and R. Falconeri (Fig.XXXIIa) respectively, possibly by the fusion and septation of the numerous filaments of the two former hairs.

Epidermis: a) Lower.

The lower epidermis is never more than one cell in depth, and the cells are always smaller than those of the upper epidermis. Their lateral walls are often sinuous, rather thick and much pitted. The folding of the walls doubtless aids in the firm attachment of one cell to another, and gives added rigidity to each cell. The cells are often papillose in structure, either the whole cell (Fig.XXXVII), or in some cases the central portion only of the cell, forming the papilla. This feature has been recorded for several species by MACFARLANE (14) and also by KOHNE (10). MACFARLANE attributes the dull green or "leaden-white" colour of the leaves of R. ciliatum and others to the

papillose formation of the epidermal cells. He describes the lower epidermal papillae in R. formosum and R. Dalhousiae as curving inwards round the stomata "so as to form very efficient wind chambers". This feature has not been observed to any appreciable extent in either of these species or in any other during the present investigation. KOHNE records "simple" papillae in R. ciliatum, R. Dalhousiae and others, and cuticular projections in R. parvifolium, but the latter have not been found. The papillose condition is found in every degree in different species from merely a highly convex outer wall (e.g. R. Cooperi) to a long tubular projection as in R. pendulum (see Fig. XXXVI). It probably aids in the illumination of the chlorophyllous tissue within the leaf, especially in cases where a thick indumentum is developed.

The level of the lower epidermis is not always uniform. In many of the large leaves where the bundles are enclosed by rigid sclerenchyma bands extending from upper to lower surface, the lower epidermis is drawn in at these points, so that the whole of the under surface forms a system of ridges and furrows (Fig.XXXVIII). In those leaves which bear peltate hairs the level of the epidermis is broken by a series of deep cavities in which the hairs are

situated. Stomata are extremely numerous on the lower surface of the leaf. When peltate hairs are present the stomata are usually localised along the sides of the cavities (see Fig.XXXIX), but are sometimes distributed over the entire surface as in R. Nuttallii.

In many small forms and occasionally in large ones (e.g. R. Griersonianum) the stomata are placed level with the surface, or nearly so (Fig. XL a). In these cases the stoma is surrounded by a few rather narrow cells which differ from the normal epidermal cells in being smaller and having straight lateral walls (Fig. XLI). In the great majority of species however the stomata project from the surface, often to a marked degree (e.g. R. argenteum, Fig.XL d). This projection is accomplished by the erection of the adjacent epidermal cells (six to eight in number) from the surrounding tissue. These epidermal cells are usually much larger than the normal ones and in extreme cases tend to become S-shaped (Fig.XL d). In a surface view they are rounded in shape, and give the appearance of a rosette round the aperture of the stoma. Fig.XLII b shows a surface view of the epidermis of R. arboreum where the adjacent epidermal cells are in focus, while the guard-cells are above and the ordinary epidermal cells below the plane of focus. In some species the adjacent epidermal cells are considerably larger than the ordinary ones, but project only slightly upwards, and distinctly inwards into

the mesophyll (R. fulgens, Fig.XL c). BREITFELD views this system of projection as an arrangement whereby, according to SCHWENDENER, not only the guard-cells, but the whole of the stomatal mechanism contracts to close the aperture.

Epidermis: b) Upper.

The upper epidermis is of two types: one-layered, or many-layered. Both types have been fully described by BREITFELD. In the former type the cells may be fairly small and thick-walled (e.g. R. primulinum, Fig.XLIII), or relatively large with thin lateral and inner walls (e.g. R. Weyrichii, Fig.XLIV). Most of the small-leaved forms of Rhododendron possess a one-layered epidermis. Gelatinisation of the internal walls of epidermal cells in some species has been recorded by several writers, including SOLEREDER. This gelatinisation occurs in R. serpyllifolium, but has not been observed by the writer in R. retusum, though VESQUE states that this species also possesses it. BREITFELD distinguishes two types of many-layered epidermis: one where the cells of the individual layers are essentially similar in structure and size, and one in which the size of the inner layers or hypoderm is much greater than that of the outermost layer. He suggests that in the former case all the inner layers have a subsidiary water-storing function, but that in the latter they are water-storers par excellence. A sequence can be traced in Figs.

XLV — XLVIII where a regular increase in size of the hypoderm cells is shown, R. retusum reaching the maximum. In a number of the Javanese species the hypoderm takes on a quite distinctive appearance, which however is probably only an advanced stage in the same sequence. Here the epidermis possesses two layers of cells, the outer being normal in size and structure, with pitted lateral walls. The inner layer is discontinuous, and the cells are usually enormously enlarged, so that they penetrate deeply into the palisade mesophyll. They are very irregular in size and possess thin pitted walls. In at least one form (Fig.XLIX), hypodermal cells of this kind, though smaller, are found on the lower surface of the leaf also. Occasionally these large cells displace some of the epidermal cells and thus come to lie directly against the cuticle (Fig. L).

R. sino-vaccinioides is an interesting form. It may be regarded as a possible transition stage between the "retusum" type of uniform enlarged cells (above the palisade cells), and the "jasminiflorum" type where the cells are very irregular and separated from one another by palisade cells. Its interest however lies in the fact that its epidermal arrangement is exactly similar to that described by Miss SMITH (21) in Erica Mackayi. In this species (Fig. LI) the hypoderm

cells are large and fairly regular, penetrating slightly into the palisade mesophyll. SOLEREDER mentions the gelatinisation of the inner walls in R. jasminiflorum, and though it has not been observed during this investigation, it would if present undoubtedly assist in the process of water absorption and storage which is carried on in these cells.

Mesophyll: a) Palisade.

BREITFELD divides the leaves of Rhododendron into two main groups according to the relative development of palisade and spongy mesophyll, i.e. i) where the palisade is strongly developed, ii) where it is only slightly developed. Examples of the first type are seen in R. Davidii and R. fictolacteum (Figs. LV & LII respectively), and in R. barbatum, R. leptothrium, R. grande and many others. In all of these the palisade tissue occupies at least one-half, and usually more, of the total depth of the leaf. In a few species this depth is occupied by only one row of much elongated cells, as in R. Davidii, but this is unusual, and the number of palisade layers is often three, and occasionally four, as in R. fictolacteum (Fig.XLII). Examples of the second group, where the development of palisade tissue is slight, are found in R. primulinum (Fig.XLIII), R. giganteum (Fig. LIII), R. sino-vaccinioides, R. serpyllifolium, R. auriculatum, etc. In R. sino-vaccinioides the leaf has a succulent appearance and the palisade layer measures only about one-eighth of the whole depth of the leaf. The cells

of this layer are unusually broad and short. In some species the palisade cells are very small and short, often not as large as the epidermal or spongy mesophyll cells (Figs.LI ,LIV). Where there are several layers, the uppermost one always shows the greatest uniformity and closeness of arrangement. Below this, the cells become more loosely arranged and often more rounded in shape, passing gradually into the spongy mesophyll (Fig. LII). Large stellate crystals of calcium oxalate are of frequent occurrence in the palisade cells of many species. In at least one species (R. jasminiflorum) slightly branched spicular cells are extremely abundant among the inner palisade cells. These cells are very thick-walled and large, and are nearly always elongated in a plane perpendicular to the leaf surface (Fig. L).

Mesophyll: b) Spongy.

The spongy mesophyll in leaves of Rhododendron is of three different kinds, and can be conveniently classified as the normal, the close and the "squared" type. The normal type, exhibited by R. primulinum, R. ciliicalyx, R. serpyllifolium and others, consists of a loose tissue irregularly arranged, and well ventilated by means of numerous intercellular spaces (Fig.XLIV). These spaces are often extremely large, and in some species run more or less vertically to the leaf surface, thus giving a fairly regular arrangement to the cells (Fig.XLIII). The spongy mesophyll cells vary in size, being rounded and smaller than

the palisade cells in R. primulinum; in R. bracteatum on the other hand they are large and more or less square or polygonal in shape.

The close type of mesophyll is similar to the normal type, but the intercellular spaces are small and infrequent, giving an unusually close texture to the tissue; this is especially noticeable in R. pendulum, and to a lesser extent in R. triflorum, R. javanicum and R. anthopogon.

The "squared" appearance of the spongy mesophyll in some of the large forms of Rhododendron is probably related to the differentiation of tissue in the stem. In the midrib of the large-leaved species there is no distinction into palisade and spongy mesophyll, but only a broad mass of tissue enclosing the bundle and differentiated into large and small cells in exactly the same way as in the cortex and pith of the stem. This tissue, passing from the stem into the leaf, gives a very characteristic appearance to the spongy mesophyll. Figs. LII , LIV are examples of this: in R. argenteum the small rounded cells form one or two almost unbroken horizontal rows, the rows being separated by extremely thin-walled large cells. In other species (e.g. R. auriculatum) the small cells are more or less isolated at the corners of the large cells and the "square" arrangement is then easily seen. These two kinds are essentially the same, and the difference in appearance is possibly due to

differences in thickness of section. Usually in this type of mesophyll the tissue becomes much closer below a vascular bundle, intercellular spaces being entirely absent. (Fig. LIV).

Midrib and lateral bundles.

The midrib varies considerably in outline, being usually very pronounced on the under surface of large leaves (see Fig.XXXVIII). It projects, however, only slightly in many smaller forms, often being flattened on the under surface, as in R. Boothii and R. anthopogon (Fig. LV a), or hardly apparent at all (Fig. LV b.c). The vascular bundle in transverse section takes the form of an inverted arch, and in the larger forms a second smaller arch is situated between the two ends of the larger (Fig.XXXVIIIb). When two arches are present they are separated by a small thin-walled pith. In extremely large leaves, for example R. giganteum, the pith is large and differentiated like the stem tissue, but this is exceptional in the genus. In smaller-leaved species the vascular tissue is almost semicircular in shape, and there is consequently no pith (Fig. LV). The xylem is radially arranged (with a few exceptions such as R. sinovaccinioides), the rows being separated at intervals by narrow medullary rays. Since the leaves in most cases persist on the plant for two or three years, a small amount of cambium is present between xylem and phloem to allow for increase in tissue. The bundle is

nearly always surrounded by a layer of sclerenchyma fibres, 5-6 cells in depth. These cells have highly thickened walls and are closely arranged without intercellular spaces. Above the bundle (on the upper side of the leaf) the palisade tissue gives way to normal parenchyma whose cells often contain calcium oxalate crystals. Below the bundle is a large mass of parenchymatous tissue, differentiated (in the majority of forms) into large and small cells in the same way as the cortex in the stem; but here both kinds of cells are thin-walled. Crystals are freqneutly found in these cells. Isolated sclereids are frequent in this region, in the petiole and lower lamina. These cells take the place of some of the large empty cells, and do not occur in the small-celled tissue which contains abundant starch.

In smaller species where there is no pith the bundle is still completely enclosed by a sclerenchyma band in many cases, e.g. R. jasminiflorum, but there is another commoner form of mechanical support in some small leaves, as in R. serpyllifolium and others. Here there is no sclerenchyma band, but the epidermal and outer mesophyll cells, usually on both sides of the bundle, possess strongly thickened walls.

The lateral vascular bundles BREITFELD places in two groups: in the first they are fibro-vascular, the fibres extending from upper to lower epidermis as in R. arboreum, R. pendulum and R. brachyanthum (see Fig. LIV); in the second the bundles are surrounded

by parenchyma and fibres are wanting, e.g. R. primulinum. Actually there is also a large group, not recorded by him, where the fibres run only from the bundle to the upper epidermis, while below the spongy mesophyll continues uninterrupted. This arrangement seems to be of commoner occurrence than that of BREITFELD's second group, and examples are R.Hodgsonii, R. decorum, R. auriculatum and many others. The vascular tissue is normal in appearance, the cells being of small size. The development of phloem is preponderant over that of xylem, and no cambium is present in the lateral bundles. The non-fibrous bundles of small leaves are surrounded by large spherical cells which form a prominent collecting-sheath (e.g. R. primulinum, R. bracteatum), and the mesophyll tissues do not vary around this, as in the larger forms. In the fibro-vascular bundles a few of these collecting cells are present laterally, linking the vascular with the mesophyll tissues.

D. DISCUSSION.

The possibility of systematic grouping, based on leaf characters, in the genus Rhododendron, has been suggested. Although the leaf as a plant organ is a variable one and can be modified in many ways by changes in the environmental conditions, yet the consistently simple outline of the leaf in the Ericaceae

is illustrative of the conservatism met with in the Order. No variation in leaf outline has been observed or can be induced in Rhododendron, and although one would hesitate to give leaf characteristics a diagnostic value, yet a consideration of them from this aspect is justifiable on account of the general stability of the leaf in the Order. RENDLE (19) states that "the leaf-anatomy (of the Order) affords characters which are found to be of value in distinguishing genera or sometimes even tribes. They are founded on the arrangement of the chlorophyll parenchyma, the presence of water-storing tissue, the arrangement of the stomata on the lower face, and the structure of the hairs." VESQUE used the types of hair, the presence or absence of gelatinisation of the epidermal cells, the presence or absence of hypoderm, and the mode of distribution of the stomata (localised or otherwise) as delimiting features between different groups. His investigation included very few species however, and his descriptions are sometimes inaccurate.

BREITFELD states that the characters of the palisade tissue is of diagnostic value between different groups of the genus. In some, according to him, there is a great development of palisade in relation to spongy mesophyll, and the cells may be either very much elongated, or rather short, and placed in several layers, one below the other. In others the palisade is less developed than the spongy mesophyll tissue. This is undoubtedly the case, and

the difference is very marked in some leaves, but there is not necessarily any similarity between two members of the same series, and there are often resemblances between two unrelated series. One must take into consideration the variability shown by the photosynthetic elements in a leaf due to external factors such as intensity of illumination. As examples of this, the structural variations in "sun" and "shade" leaves, and the development in many cases of palisade tissue on the abaxial surface induced by torsion of the petiole, may be cited. For this reason a character such as that suggested by BREITFELD cannot be regarded as indicative of relationships.

The structure of the hairs can sometimes be used as indicators of affinity, and in a very few cases may perhaps be specific. The genus can be divided into two large groups, according to whether the species are lepidote (possessing peltate hairs) or elepidote. In some cases also the structure of the peltate hair itself (e.g. the relative sizes of the central umbo and annular membrane) is probably of specific value. Up to the present the type of hair of R. pendulum has been found only in this species, but further examination may reveal it in others. In very many cases, species from different series possess the same kind of hair (e.g. R. anthopogon and R. ledoides, R. decorum and R. obtusum), and two closely related species may show totally different

hairs (e.g. R. bullatum and R. pendulum). Thus, until a more comprehensive survey is made of the species within this genus, none of the leaf characters can be regarded as definitely specific, or even as diagnostic of a single series.

IV. EXAMINATION OF THE STEM FOR THE PRESENCE OF AN ENDODERMIS AND THE ORIGIN OF THE PHELLOGEN.

IV. EXAMINATION OF THE STEM FOR THE PRESENCE OF AN ENDODERMIS AND THE ORIGIN OF THE PHELLOGEN.

In a paper dealing with the anatomical peculiarities characteristic of peat plants, PRIESTLEY (15) describes as typical features the large amount of fat present in the tissues, and the presence of a conspicuous "secondary" endodermis in the stem, particularly of ericaceous plants. The term "secondary endodermis" has been used by KROEMER to denote one whose cell walls are thin but have usually a suberin lamella over the whole inner surface. The presence of both of these features is claimed by PRIESTLEY to be the result of a metabolism peculiar to plants growing in an acid or peaty soil, during the process of which large quantities of fatty acids are liberated. In a later paper by the same author (16) the presence of this functional endodermis is considered to be the causal factor determining the origin of the phellogen within the pericycle. An investigation of the stem anatomy of Rhododendron proves that this plant does not conform with PRIESTLEY's claims. The following is a list of the species examined for the presence or absence of an endodermis and the origin of the phellogen. In every case the stems examined were taken from the base of the current year's growth, and sections were stained in Sudan III:

Species	Endodermis	Phellogen
R. adenogynum	none	pericyclic
R. aechmophyllum	none	"
R. agglutinatum	none	"
R. apodectum	none	"
R. argyrophyllum	none	"
R. auriculatum	none	"
R. australe	none	"
R. austrinum	an incomplete endodermis in very young stems: none later.	"
R. Balfourianum	none	"
R. Beesianum	none	"
R. Boothii	none	"
R. brachyanthum	none	"
R. bullatum	none	"
R. callimorphum	none	"
R. camelliaeflorum	none	"
R. Campbelliae	none	"
R. Campylocarpum	none	"
R. cephalanthum	numerous isolated cells stain	"
R. chartophyllum	none	"
R. chasmanthoides	none	"
R. chryseum	none	"
R. colletum	none	"
R. complexum	numerous isolated cells stain	"
R. crassum	none	"
R. cuneatum	none	"

Species	Endodermis	Phellogen
R. cyanocarpum	none	pericyclic
R. Davidii	none	"
R. Davidsonianum	none	"
R. Delavayi	none	"
R. desquamatum	none	"
R. detonsum	none	"
R. Edgeworthii	none	"
R. eriogynum	none	"
R. euchaites	none	"
R. eudoxum	none	"
R. facetum	none	"
R. Fargesii	none	"
R. ferrugineum	none	"
R. fictolacteum	none	"
R. flavidum	none	"
R. fulgens	none	"
R. galactinum	none	"
R. Genestierianum	none	"
R. glancophyllum	occasional isolated cells stain	"
R. Griersonianum	none	"
R. hippophaeoides	an incomplete endodermis in very young stems: none later.	"
R. Hookeri	none	"
R. hypolepidotum	none	"
R. impeditum	an incomplete endodermis in very young stems: none later.	"
R. irroratum	none	"

Species	Endodermis	Phellogen
R. Kaempferi	none	pericyclic
R. Keysii	none	"
R. ledifolium	none	"
R. leptothrium	none	"
R. Lindleyi	none	"
R. linearifolium	none	"
R. longistylum	an incomplete endodermis in very young stems: none later.	"
R. lukiangense	none	"
R. lutescens	none	"
R. Maddenii	none	"
R. megeratum	none	"
R. mollicomum	none	"
R. mucronulatum	none	"
R. nematocalyx	none	"
R. niphargum	none	"
R. obtusum	none	"
R. Oldhamii	none	"
R. oleifolium	none	"
R. oreodoxa	none	"
R. oreotrephes	none	"
R. oreotrephoides	none	"
R. orthocladum	an incomplete endodermis in very young stems: none later.	"
R. peramoenum	none	"
R. polylepis	none	"
R. poukhanense	none	"

Species	Endodermis	Phellogen
R. primulinum	none	pericyclic
R. prophantum	none	"
R. racemosum	none	"
R. rhantum	none	"
R. rupicolum	an incomplete endodermis in very young stems: none later.	"
R. Sargentianum	none	"
R. Searsiae	none	"
R. serpyllifolium	an incomplete endodermis in very young stems: none later.	"
R. Sheltonae	none	"
R. spinuliferum	none	"
R. Spooneri	none	"
R. Sublanceolatum	none	"
R. sulfureum	none	"
R. supranubium	none	"
R. tapeinum	none	"
R. telmateium	none	"
R. Thomsonii	none	"
R. Traillianum	none	"
R. triflorum	none	"
R. Veitchianum	none	"
R. Vilmorinianum	none	"
R. Weyrichii	none	"
R. yanthinum	none	"
R. yedoense	none	"
R. yunnanense	none	"

Although fatty substances are present in the phloem and cortex in the stems of these species, and the epidermis is highly cuticularised, it will be seen that no endodermis is present in the great majority of species. Those species which possess endodermal cells are the small heath-like forms such as R. hippophaeoides and R. serpyllifolium, and even here the endodermal cylinder is by no means complete. A curious feature in these forms is the presence of an apparently "secondary endodermis", usually incomplete, in the very young parts of the stem, and the complete or partial disappearance of this in the older portions, all within one year's growth. For this reason these species have been described as having "an incomplete endodermis in very young stems: none later." In a great many of the larger forms of Rhododendron isolated cells immediately outside the pericyclic fibres have frequently been found to stain with Sudan III, while other stems from the same plant showed a complete absence of these. The cells showed no trace of Casparian thickening, and cannot be considered as endodermal in character. They are undoubtedly the first cells to become suberised in the process of cork formation which is described in the following section.

In spite of these facts the phellogen is in all species pericyclic in origin. It has been shown in a later paper by PRIESTLEY (17) that the pericyclic cork in the stem of Camellia japonica is determined,

in the absence of an endodermis, by a sclerenchymatous layer at the inner limit of the cortex. This sclerenchyma tissue has the form of a continuous cylinder, or short thick-walled elements arranged so as to exclude intercellular spaces. Accumulations of organic solutes takes place within this layer, and PRIESTLEY considers this to be the determining factor in the initiation, in this region, of meristematic activity. All species of Rhododendron possess a layer of sclerenchyma fibres in a similar position in the stem, but here they cannot be considered effective in determining the origin of the phellogen, since in most cases they are grouped in discontinuous masses (Fig.LVIII), and occasionally they do not reach their full development until some time after that of the cork cells themselves.

Cork Formation in Rhododendron.

The formation of cork in the stem of most species of Rhododendron is unusual and interesting. It has been seen from the preceding section, and has also been recorded by VESQUE that the phellogen normally arises within the pericycle immediately internal to the fibres. This phellogen lays down a cork layer at an early stage in the green stem, usually developing first immediately within the gaps between the fibre masses. It quickly forms a continuous cylinder, 2-3 cells wide, of suberised rectangular cells, completely enclosing the stele, often, in a very young stem, before the pericyclic fibres are

fully developed. In a few species such as R. primulinum, R. obtusum and R. longistylum, this cork layer apparently acts as an effective barrier between stele and cortex; the latter is cut off from the vascular supply and dies off gradually down the stem. This is evident on the external surface of the stem sometimes as a gradual transition or sometimes as a definite junction of green and brown colour. The species which show only this pericyclic cork appear to be those which possess a very narrow cortex and a particularly early development of cork in the young stem. In R. primulinum, for example, the cork layer when fully developed (3-4 cells wide) may measure as much as half the width of the entire cortex (Fig. LVI), while in large stems like that of R. fulgens the width of the cork layer is about 1/40 or less of that of the cortex.

This effect, however, produced on the cortex by the pericyclic cork alone, seems to be exceptional. The majority of stems show a sharp junction of green living tissue and brown withered bark, usually in the basal part of the last year's growth. This junction runs often very irregularly round the stem, sometimes extending for several inches up on one side (Fig. LVII). Below the junction, patches of green living tissue, varying in size, can often be seen enclosed in the dead bark (Fig. LVIIa). These occur sporadically and are sometimes though not necessarily connected with old leaf- or bud-traces. The bases of the older

leaves are often surrounded by similar small areas of green tissue in a stem which is otherwise completely brown: these gradually turn brown some time after the leaf has fallen.

Transverse sections taken across the junction of green and brown tissue from above downwards show a remarkable development of cortical cork. A considerable time after the pericyclic cork layer is complete, the cells between the pericyclic fibre masses on one side of the stem, and then those immediately external to them, become lightly suberised (Fig.LVIII): these cells are distinguishable by staining the section in Sudan III, and may easily at this stage be mistaken for isolated endodermal cells. Division of the cells in a tangential direction is initiated and each of the sclerenchyma masses affected thus becomes enclosed by a small layer of cork, two to three cells in depth. Gradually every fibre mass in the stem becomes surrounded in this way (Fig. LIX). The inner cortical cells immediately external to this cork layer become closer in texture and densely packed with starch. As one passes lower down, almost into the brown portion of the stem, a similar meristematic activity is seen to arise in the central and outer cortex, on the side of the stem where the cork originated (Fig.LX,LXI). Since the activity arises further and further out as one passes lower down the stem, the cortex enclosed is cut off in all directions from communication with other tissues and rapidly dies.

Eventually as the outermost cortex is affected the phellogen is seen to have the form of two arcs, placed on opposite sides of the stem, and taking a curved oblique course through the cortex from the pericyclic cork cylinder to the epidermis (Fig. LX): in this way a large area of cortex and epidermis is isolated and this rapidly dies. New phellogen layers continue to arise in the still living cortex, running from between each fibre mass to the epidermis. Sometimes two or three can be seen in close proximity (Fig. LXII vi), and each is accompanied by an accumulation of starch in the adjacent living cortical cells. Fresh arcs of cortical tissue are thus isolated, until the two phellogen layers meet and unite immediately within the epidermis on the opposite side of the stem from which they arose. At this point the whole of the external surface of the stem appears brown, a small patch of central cortex being the only living tissue left outside the stele (Fig. LXII viii). This decreases in size as one passes down, and the final stage of the activity is seen in the small patch of suberised cortical cells at the base of the junction. The whole of the cortex below this level is completely dead and devoid of contents, and forms normal bark.

The point of interest in this method of cork formation lies in the peculiar development of repeated phellogen layers in a cortex which is still

green and living for an indefinite period after the completion of a pericyclic cork cylinder. These layers may form either in rapid succession or very gradually, giving respectively the circular or extremely irregular junctions seen on the external surface of the stem. For this phenomenon two alternative explanations may be suggested: either the cork cells formed by the pericyclic phellogen cannot be completely impermeable to the outwards transmission of supply from the vascular tissues, or else the extent of vertical conduction in the cortical cells (i.e. downward transmission from a younger region of the stem where no pericyclic cork has yet developed) is greater than has hitherto been supposed.

SUMMARY

I. The morphology of the seed and seedling of some species of Rhododendron is described. The uniformity of structure exhibited is discussed and the conclusion drawn that within Rhododendron the specific peculiarities shown by the adult plant are not reflected in the seedling.

II. The morphology of the adult plant, including the nodal anatomy, is described. The external and internal morphology of the leaf is dealt with in detail, and the diagnostic value of some structural features discussed.

III. The absence of an endodermis and the pericyclic origin of the phellogen in the stem is recorded, and an unusual subsequent development of cortical cork described.

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VII. FIGURES.

Fig. I. Drawing to illustrate differences of shape, size and structure in seeds of Rhododendron: (a) *R. sino-vaccinioides*, (b) *R.discolor*, (c) *R.oleifolium*, (d) *R.Cooperi*, (e) *R.Fauriei*, (f) *R.pseudo-yanthinum.* X 15.

FIGURE I.

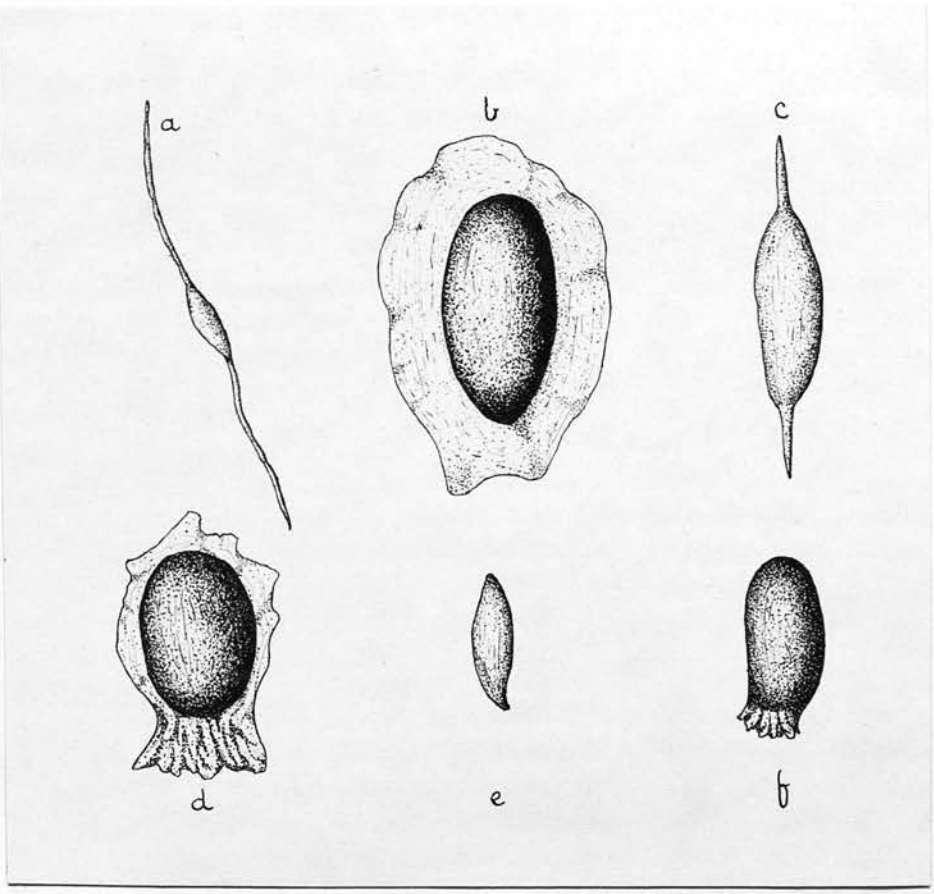


Fig. II. Portion of the testa of R. decorum showing elongated tapering cells, with thickened lateral walls and finely pitted surfaces. Camera Lucida, x 270.

FIGURE II.

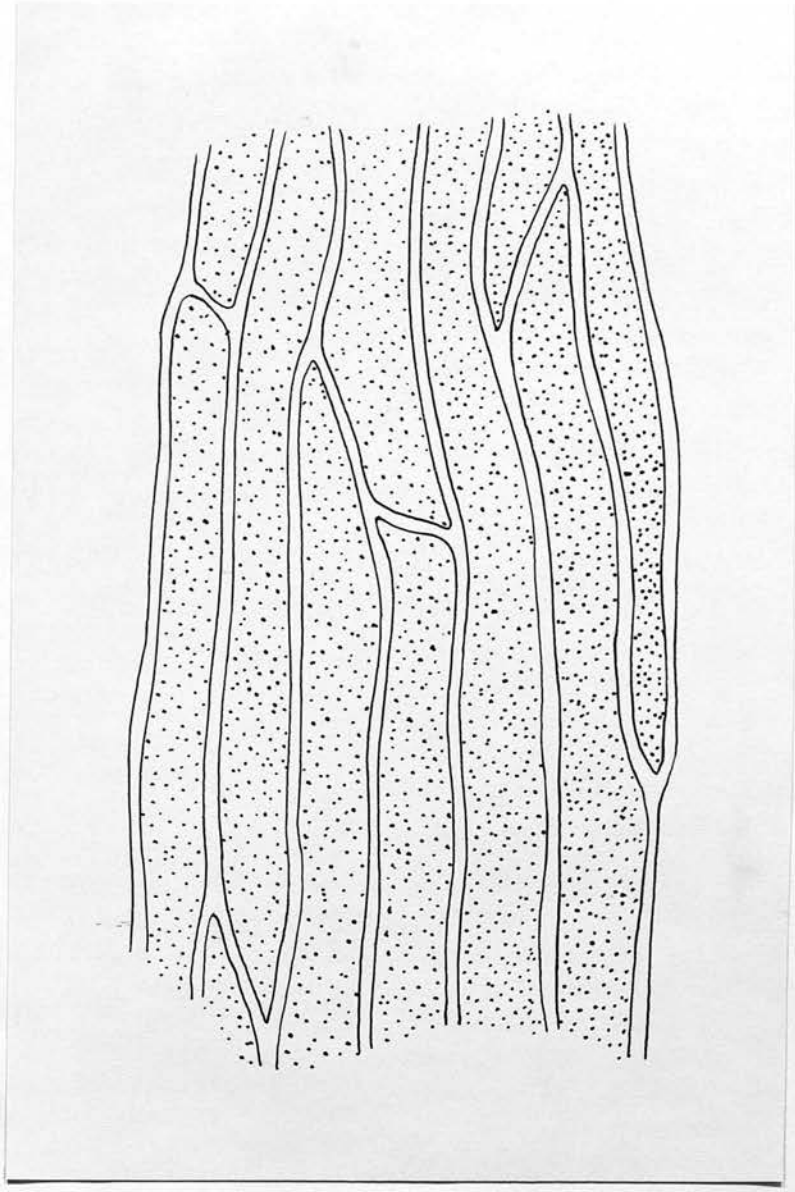


Fig. III. Longitudinal section of a seed of R. decorum: c = cotyledon, p = plumule, e = oily endosperm, hr = hypocotyl and radicle, t = testa. Camera lucida, x 60.

FIGURE III.

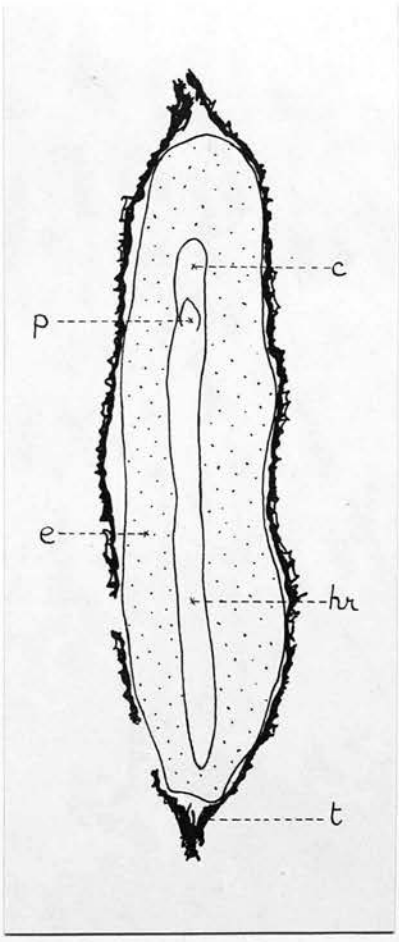


Fig. IV. Stages in the germination of Rhododendron, x 8.

FIGURE IV.

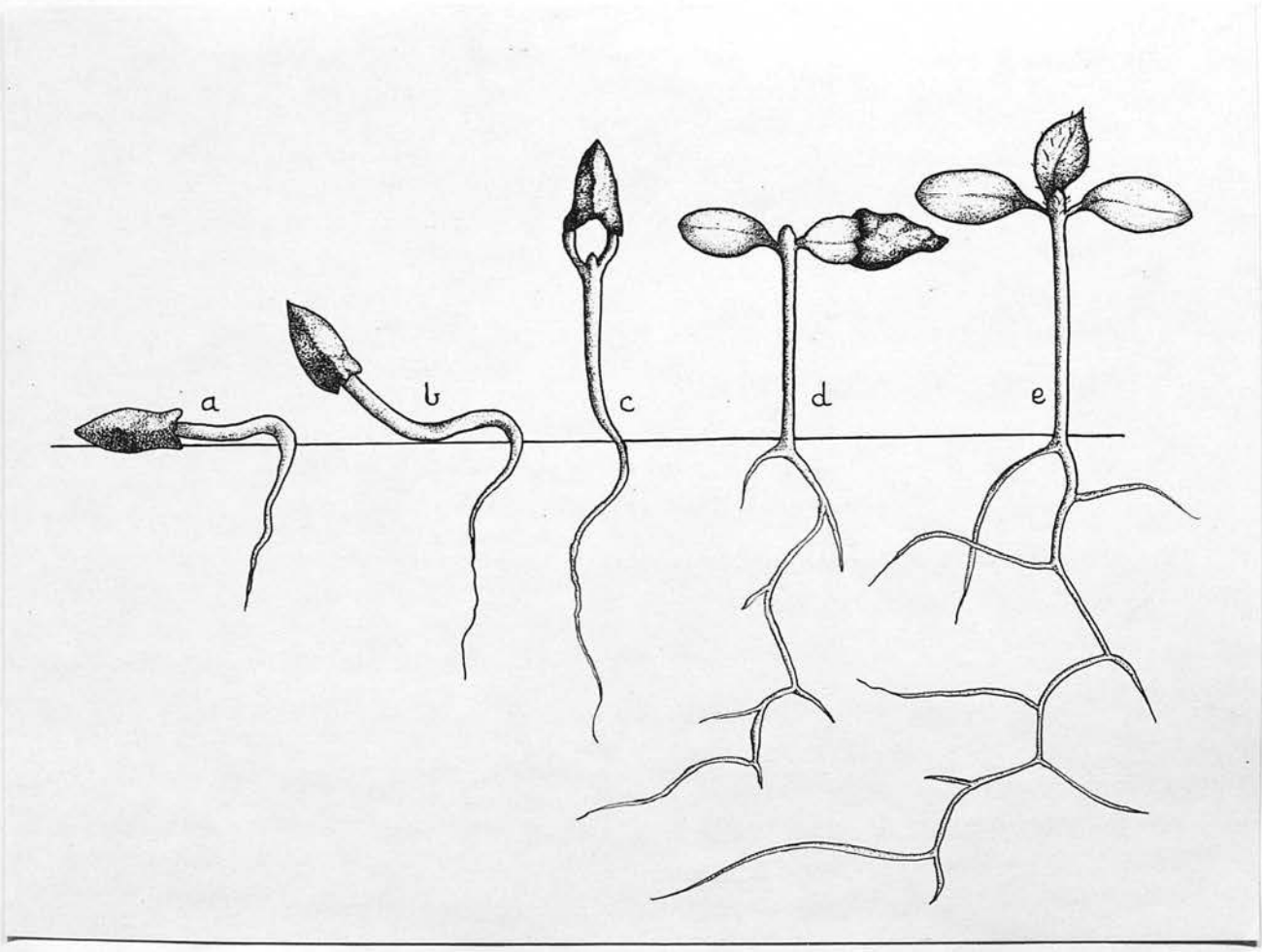


Fig. V. Transverse sections across the hypocotyl and epicotyl of a Monocotylous seedling of R. Cooperi: (a) across the upper hypocotyl, (b) across the hypocotyl and cotyledonary base, (c) across the epicotyl and cotyledon. Vascular tissue indicated by cross-hatching. Note the cotyledonary bud-trace, and the abundance and size of the peltate hairs. Camera lucida, x 270.

FIGURE V.

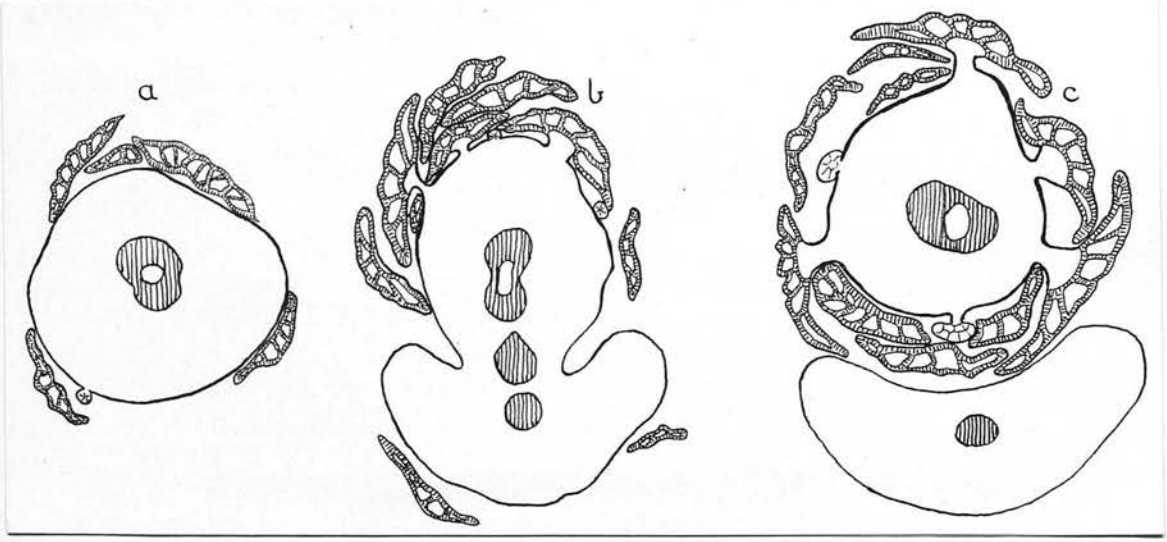


Fig. VI. Abnormal seedlings: a - d, seedlings of R. arboreum, showing (a) unequal cotyledons, (b) one slightly lobed cotyledon, (c) one bilobed cotyledon, (d) three equal cotyledons: (e) seedling of R. discolor showing partial syncotyly and schizocotyly, (f) tricotylous seedling of R. campanulatum, (g) and (h) tricotylous seedlings of R. triflorum. x 7.

FIGURE VI.

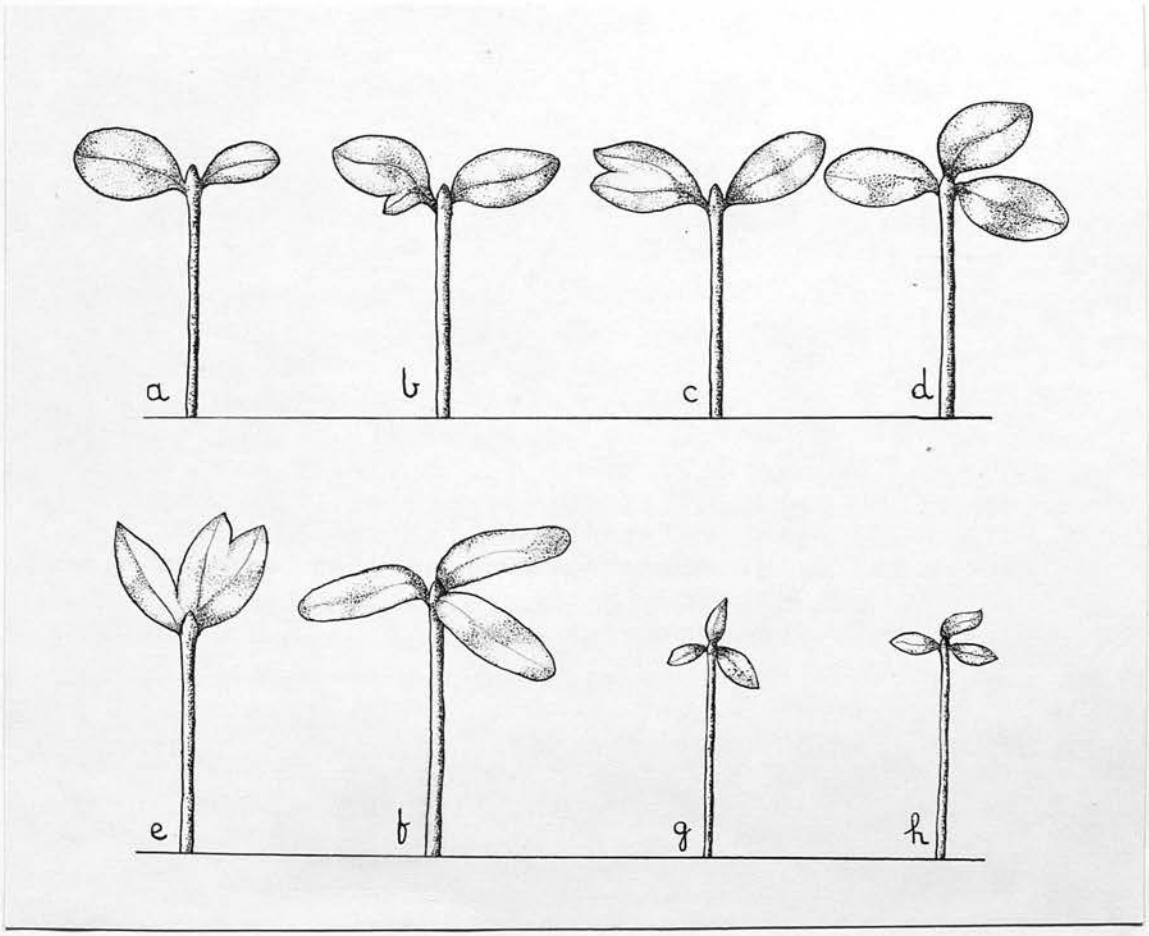


Fig. VII. Diagram to show transverse sections across the hypocotyl of a tricotylous seedling of R. campanulatum: (a) three cotyledons and young epicotyl, (b) fusion of two cotyledons, (c), (d) and (e) junction of cotyledons to the hypocotyl and entry of the traces, (f) - (l) gradual disappearance of one trace, and rounding of the stele to give normal structure of lower hypocotyl.

FIGURE VII.

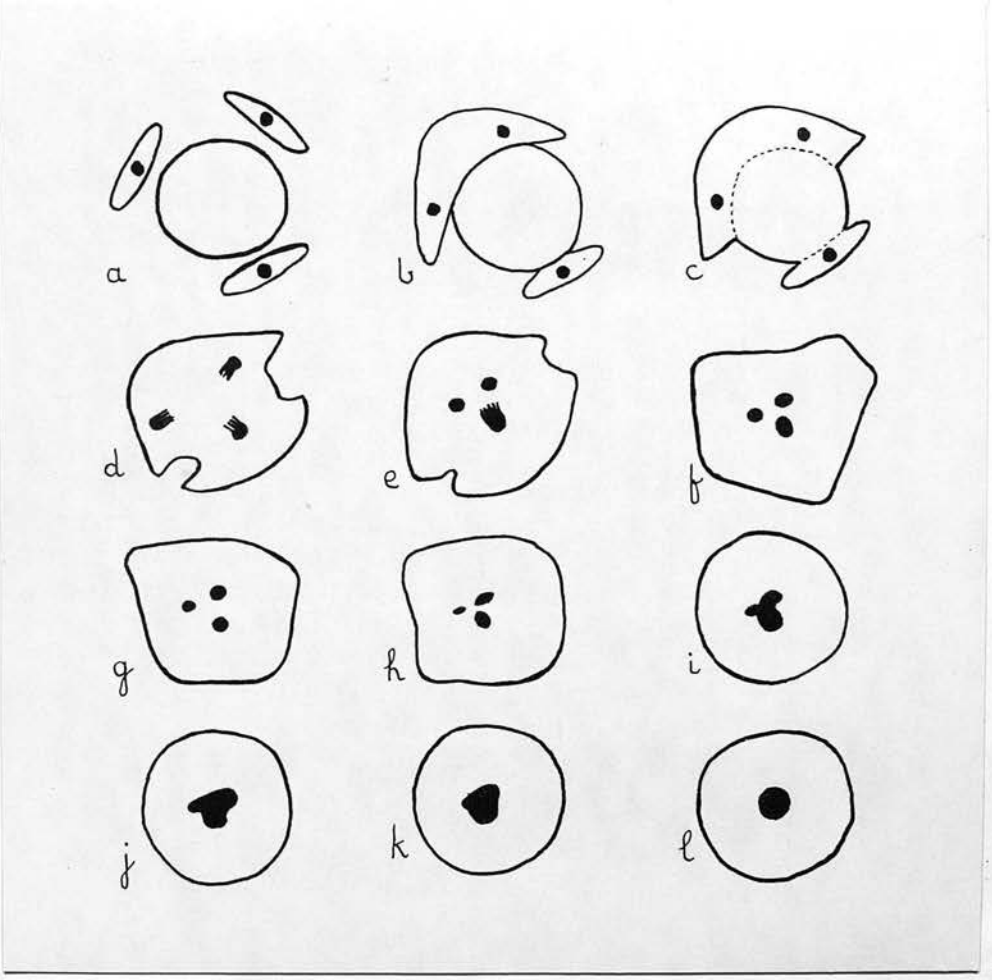
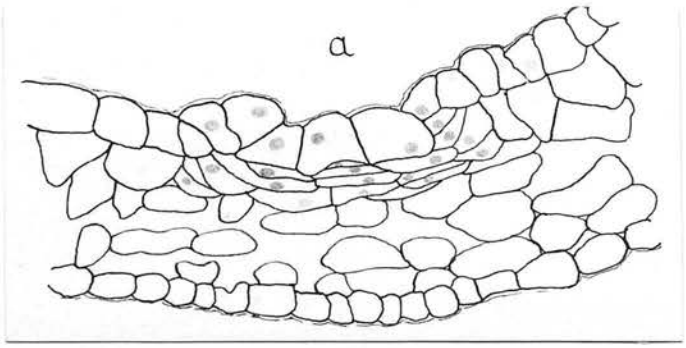
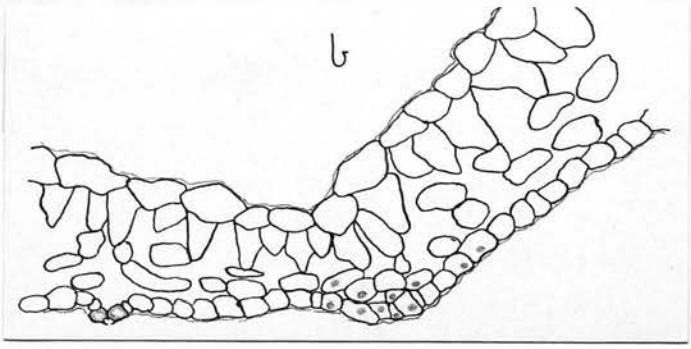
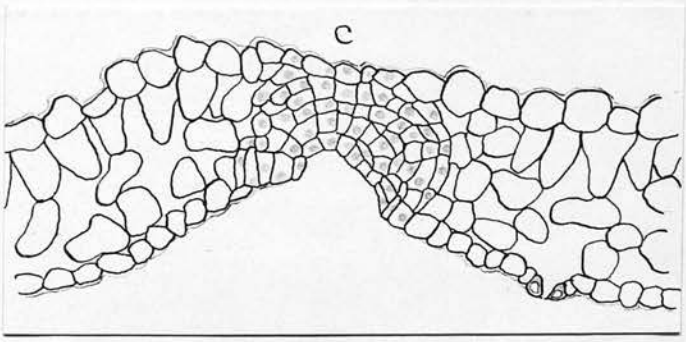


Fig. VIII. Tranverse sections, from below upwards, across the central part of a lobed cotyledon from an abnormal seedling of R. discolor: (a) slight meristematic activity on the upper surface, (b) beginning of activity on the lower surface and disappearance of it on the upper, (c) beginning of the lobing of the cotyledon, (d) final stage in the lobing. Camera lucida, x 270.

FIGURE VIII.







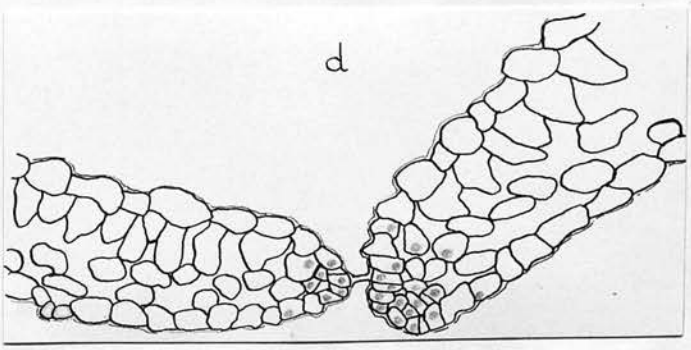


Fig. IX. Transverse section of the central portion of a young cotyledon of R. decorum, showing small median bundle, and projecting stomata on the lower surface. Camera lucida, x 270.

FIGURE IX.

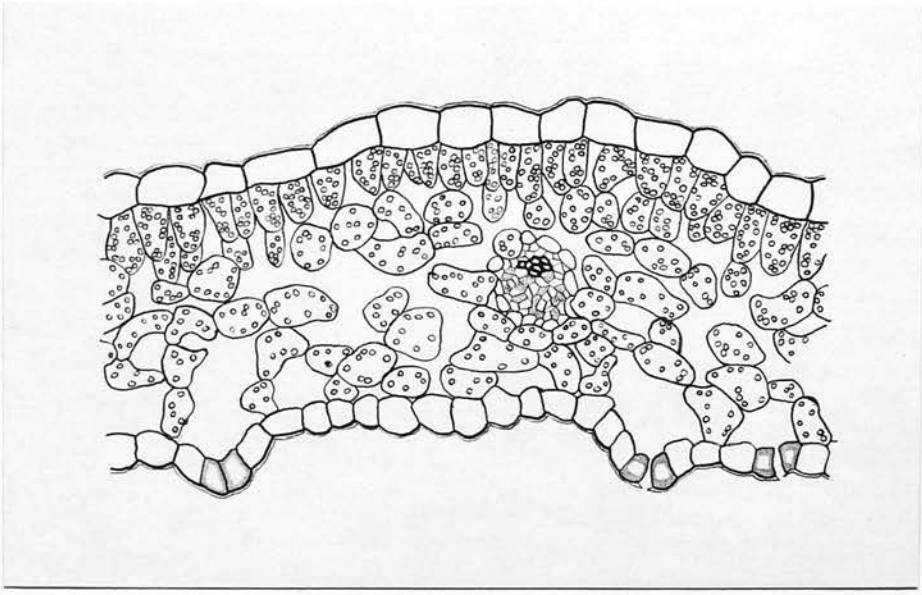


Fig. X. Margin and portion of the lower epidermis of a cotyledon of R. decorum, showing sinuous lateral walls of the epidermal cells, marginal and surface stomata, and two types of marginal hair. Camera lucida, x 270.

FIGURE X.

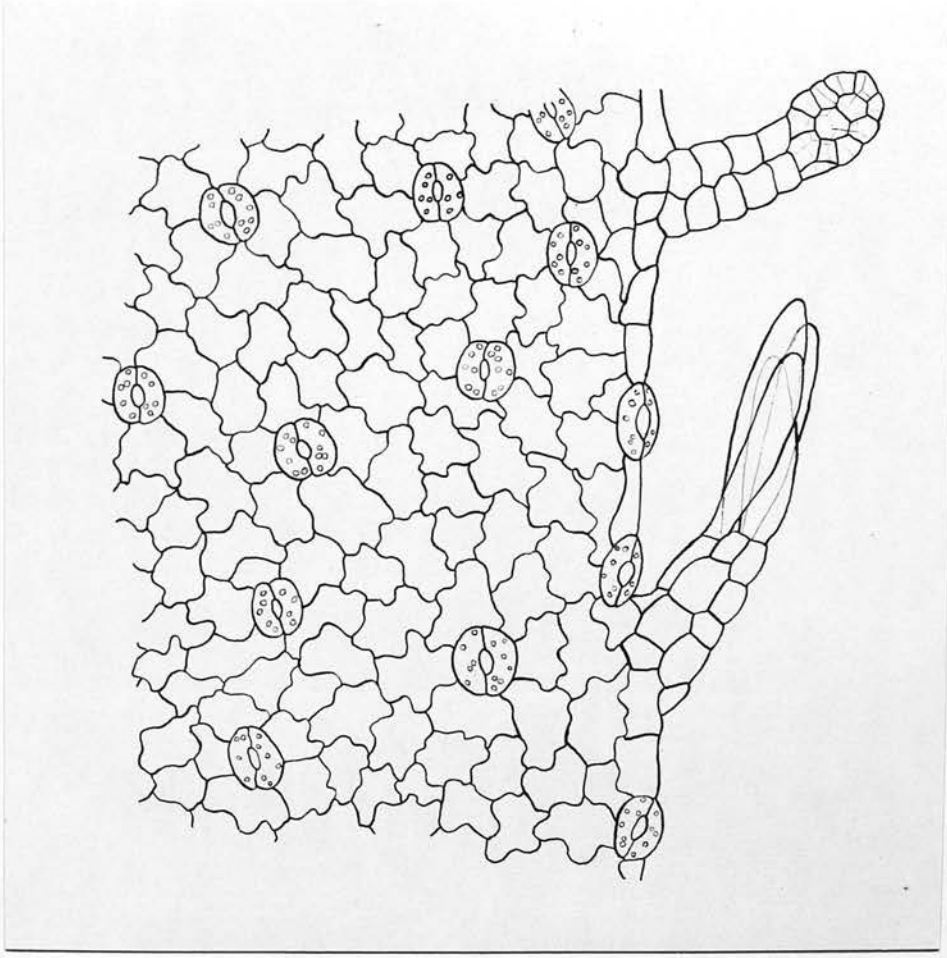


Fig. XI. Diagram showing the movement of the vascular strands during transition from root to stem structure: xylem in black, phloem in cross-hatching. (After Eames and Macdaniels).

FIGURE XI.

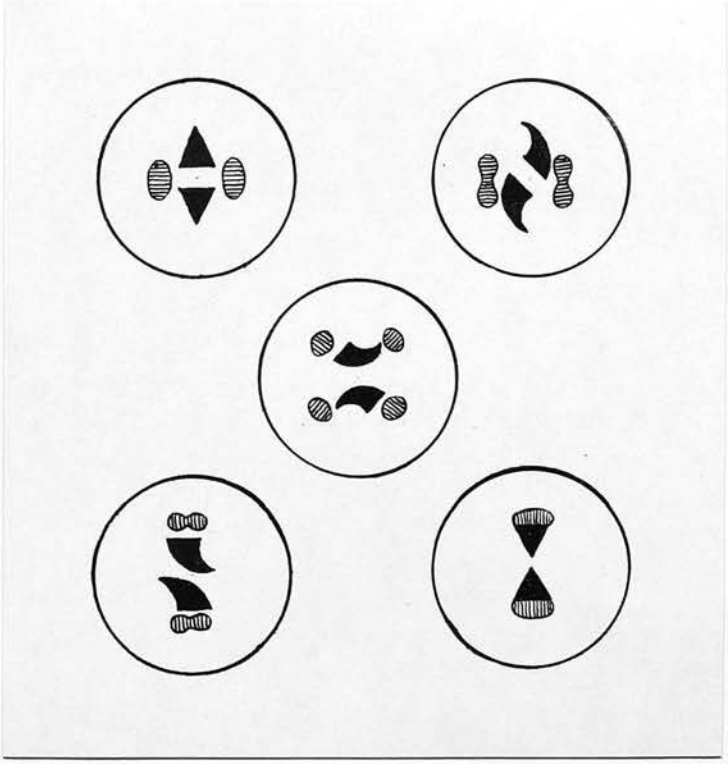


Fig. XII. Transverse section of the upper hypocotyl of R. decorum, showing division and movement of the phloem strands during transition from root to stem structure. Note the abundance of tannin-granules in the epidermal cells. Camera lucida , x 300.

FIGURE XII.

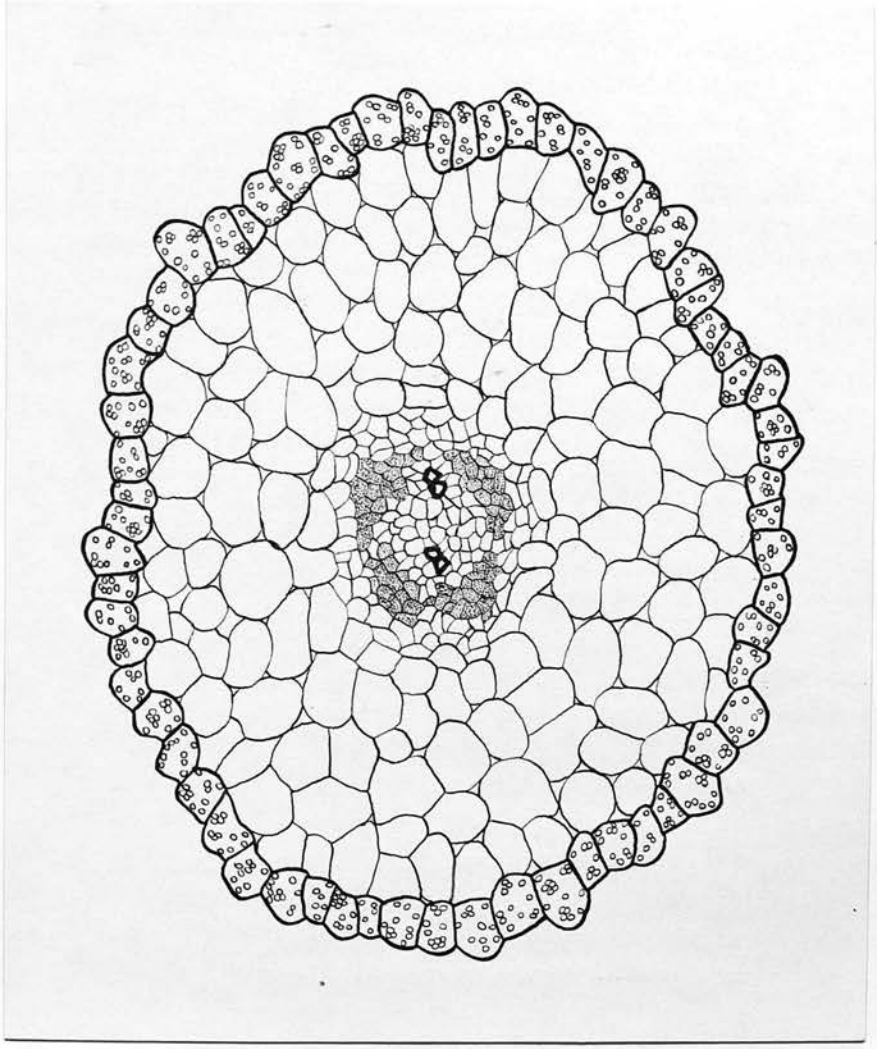


Fig. XIII. Transverse section of the hypocotyl of R. campanulatum, showing a central diarch strand of xylem, and a central secretory canal in each phloem strand. Note the large intercellular spaces in the cortex, and the fine ridges on the epidermal cell walls. Camera lucida, x 300.

FIGURE XIII.

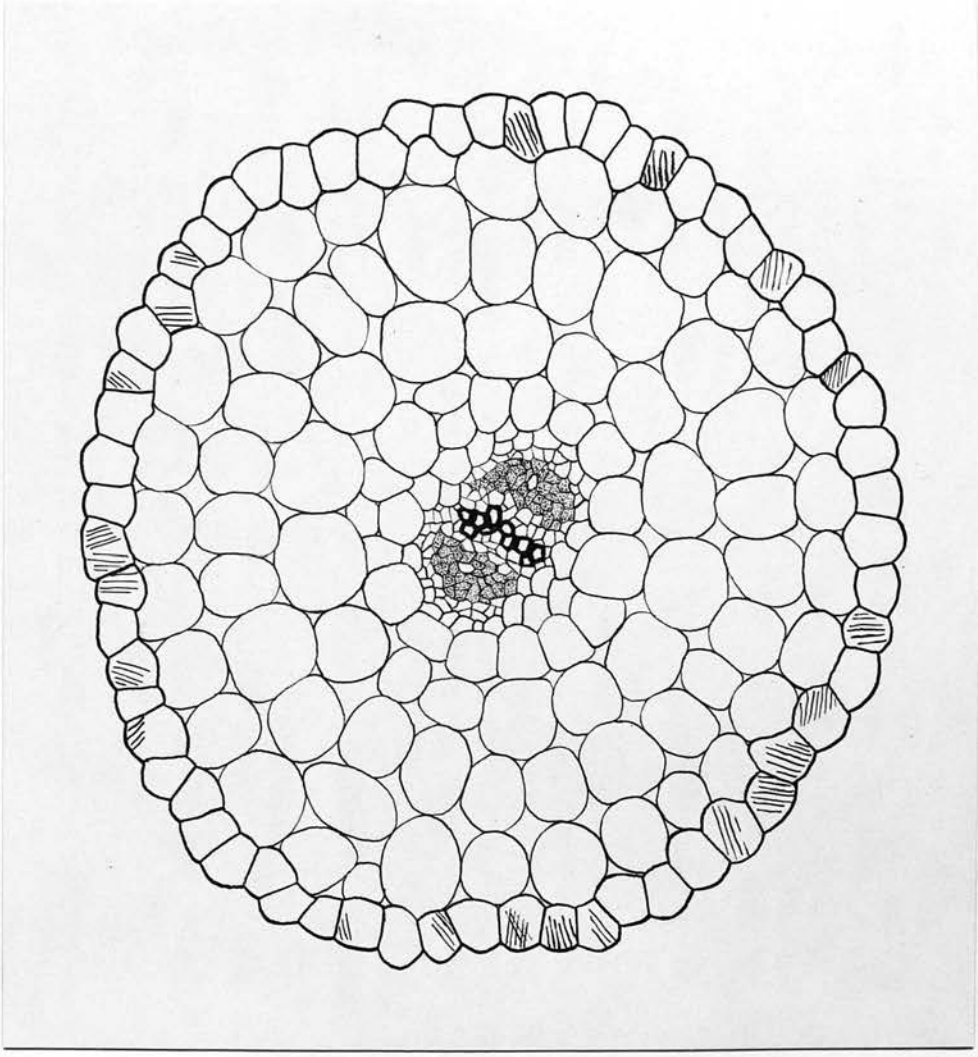


Fig. XIV. Transverse section of a few epidermal cells from the hypocotyl of R. Wadanum, showing the papillose nature of many of them. Camera lucida, x 270.

FIGURE XIV.

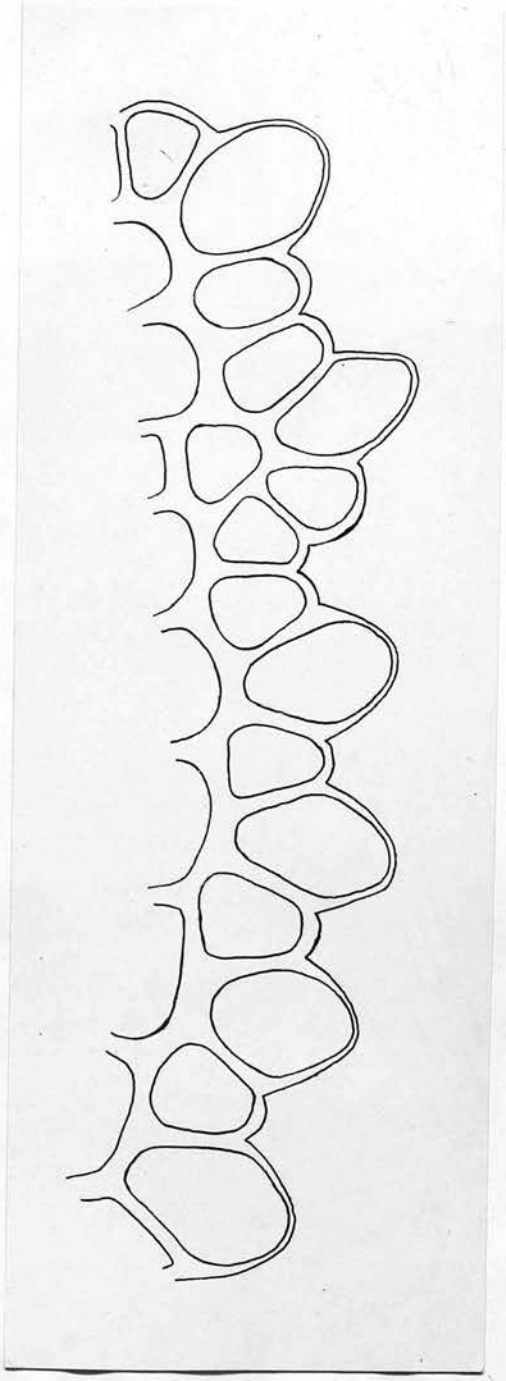


Fig. XV. Transverse section of a young seedling root of R. decorum showing a small diarch stele. Note the thickening on the radial and inner tangential walls of the single-layered cortex, and the very large cells of the limiting layer.

FIGURE XV.

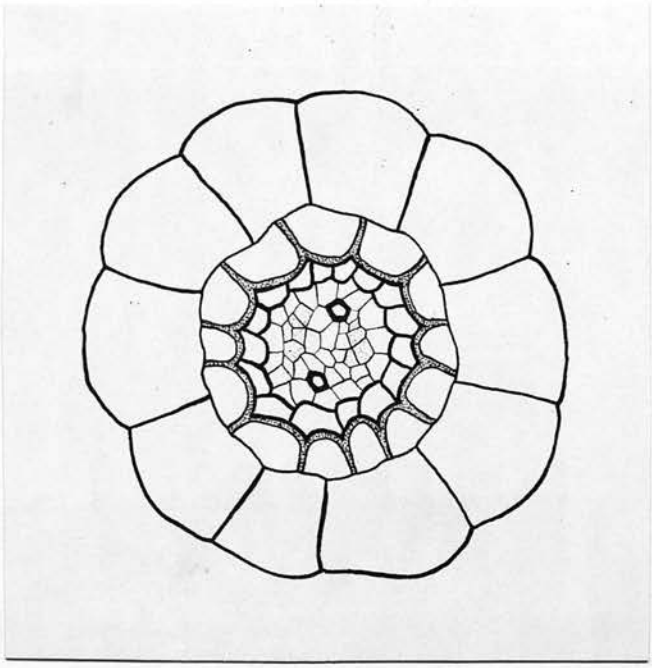


Fig. XVI. Epidermal cells from the root and hypocotyl of R. decorum, showing mycorrhizal infection: (a) - (c) root cells, surface view, (d) hypocotyl cell, transverse section. (a) showing an advanced stage in digestion of the fungal hyphae, (b) and (d) showing normal infection, (c) an early stage in digestion showing the grouping of the hyphae round the enlarged cell nucleus. Camera lucida, x 300.

FIGURE XVI.

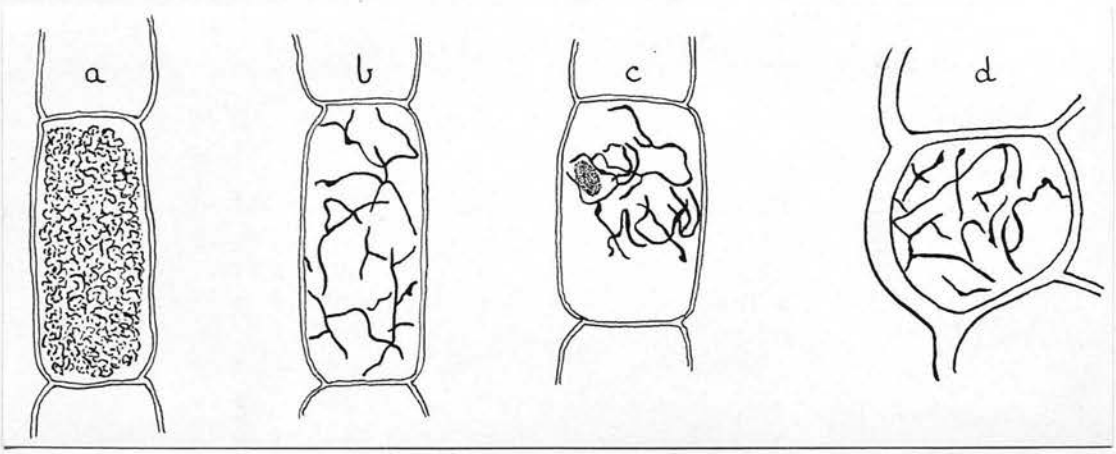


Fig. XVII. Transverse section of a seedling root of R. ambiguum, showing an early stage in lateral root formation: s. = stele, c = cortex and limiting layer, e = endodermis, of main root, r = root-cap of lateral root. Camera lucida, x 270.

FIGURE XVII.

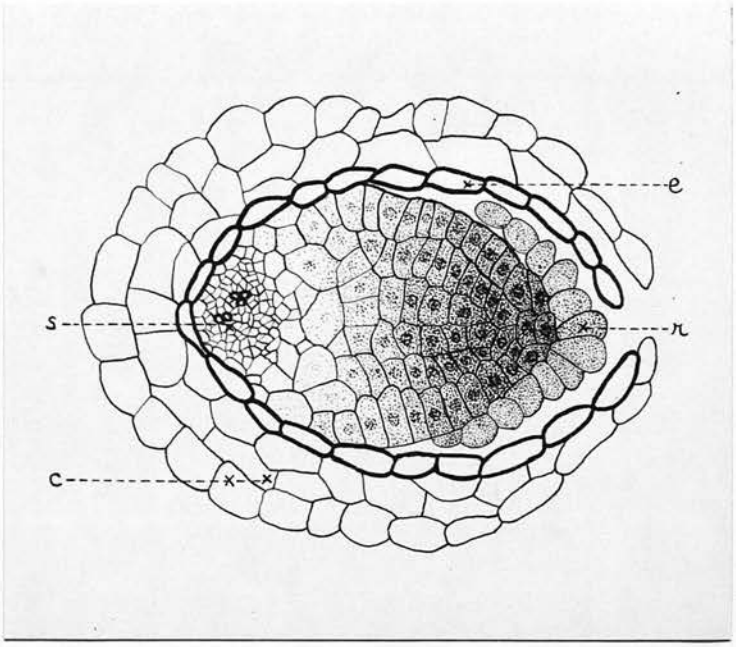


Fig. XVIII. Transverse section of the epicotyl of a young seedling of R. decorum, showing two primary xylem strands, an early stage of secondary growth, and a slight differentiation of tissue in the cortex. Camera lucida, x 270.

FIGURE XVIII.

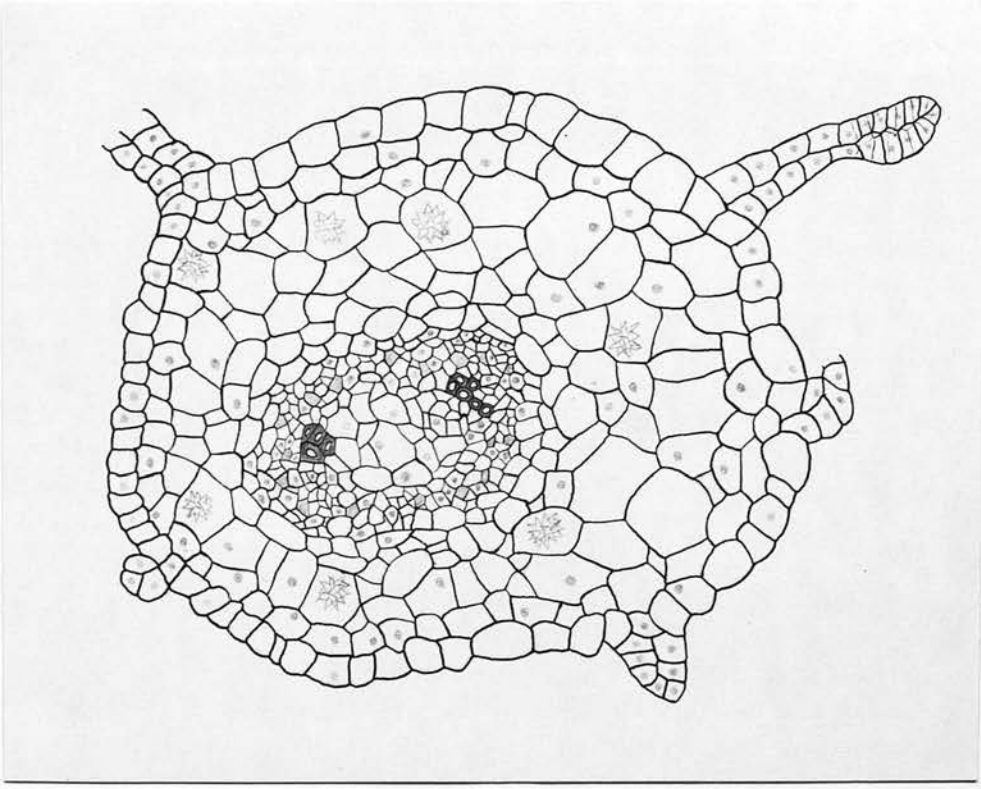


Fig. XIX. Four types of hair occurring in cotyledons of Rhododendron: (a) (b) and (b1) marginal multicellular hairs of R. decorum, (c) surface peltate hair of R. calostrotum, (d) marginal unicellular hair of R. primulinum. Camera lucida, x 270.

FIGURE XIX.

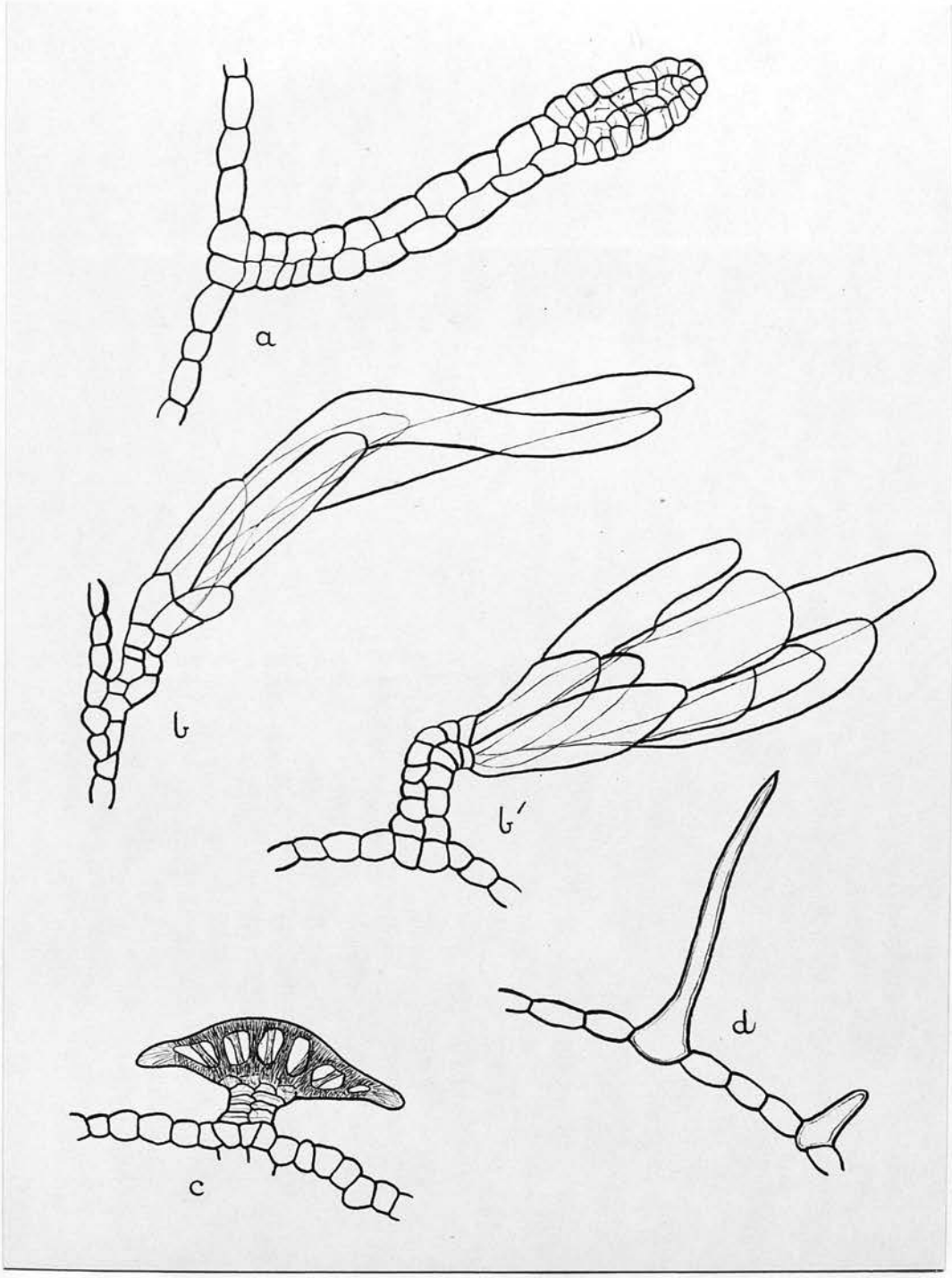


Fig. XX. Midrib and lateral vein of a twelve-months-old leaf of R. decorum, seen in transverse section. Note the radial arrangement of the xylem in the midrib, and the sclerenchymatous tissue on the upper and lower sides of each bundle. Freehand, x 150.

FIGURE XX.

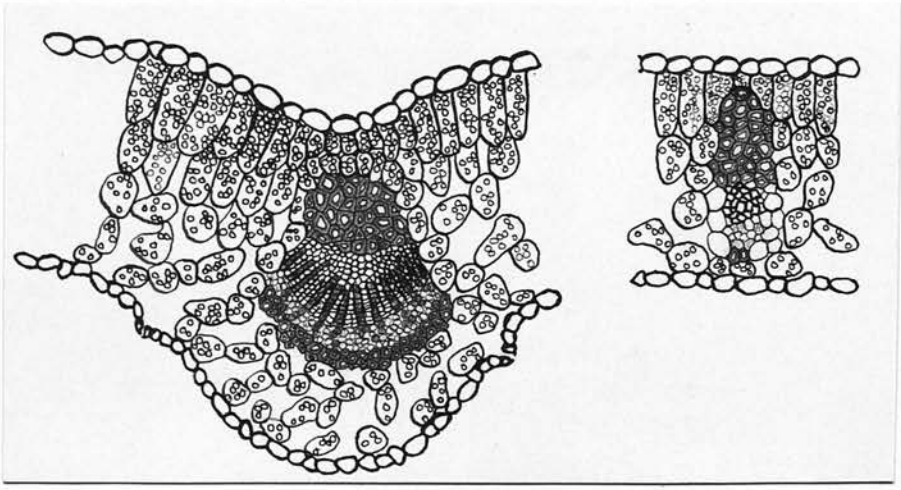


Fig. XXI. Portion of a twelve-months-old hypocotyl of R. decorum: b = bark, p = thick-walled phloem, m = medullary ray, x^1 = secondary xylem, x = primary xylem. Partly camera lucida, x 270.

FIGURE XXI.

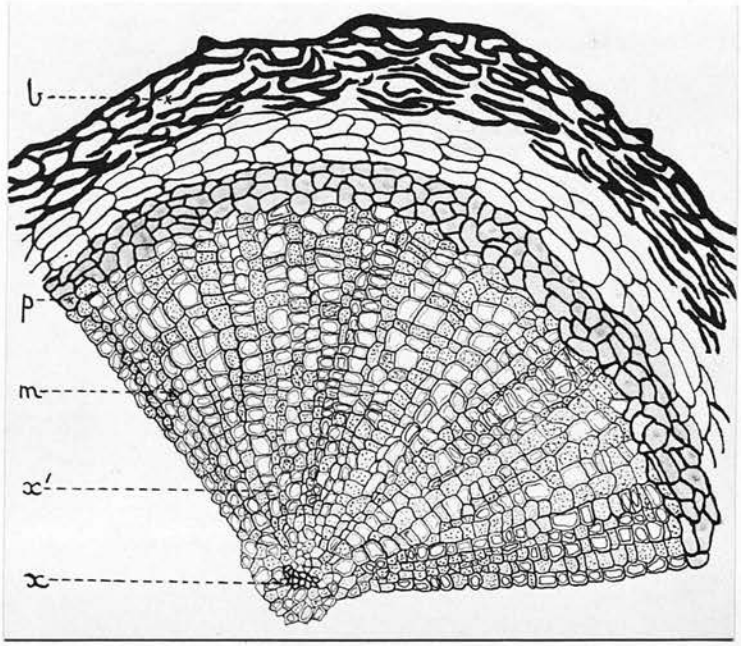
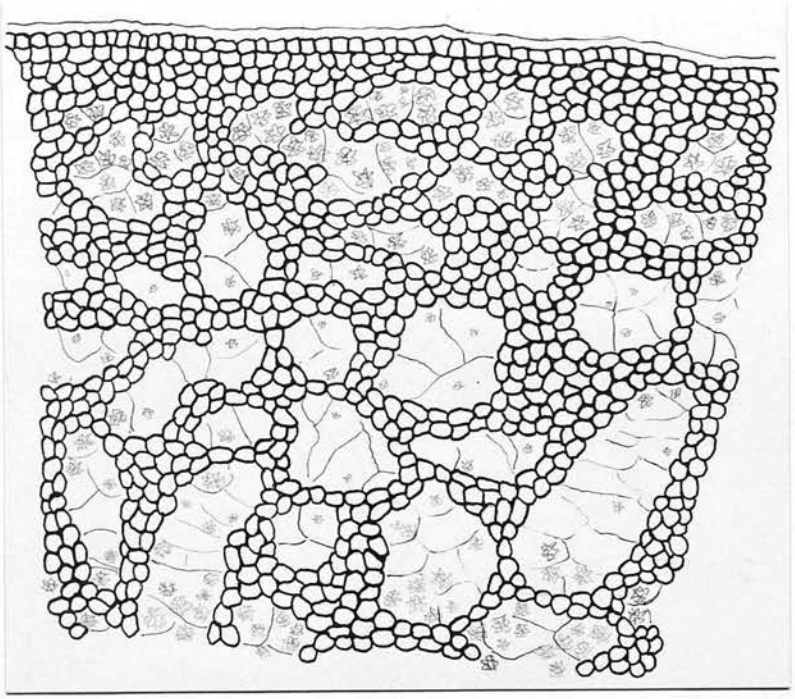
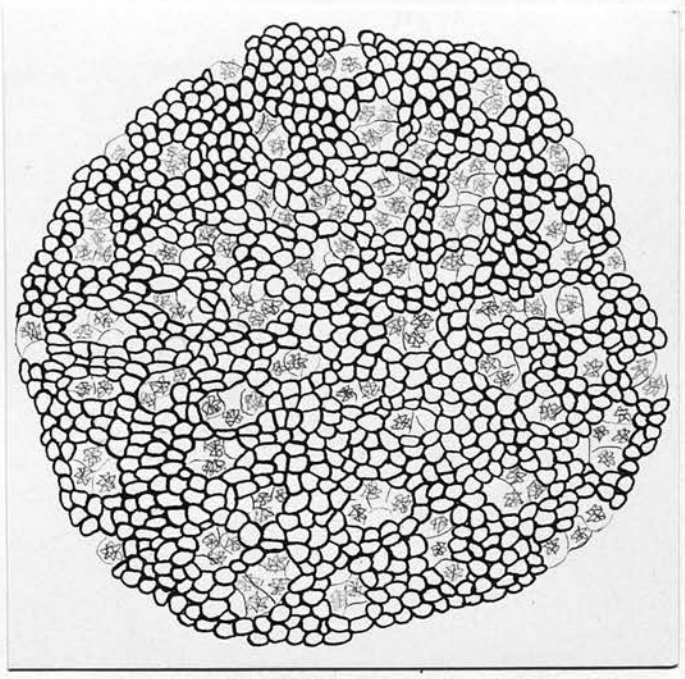


Fig. XXII. Transverse sections of (a) the cortex, (b) the pith, in the young adult stem of R. decorum, showing differentiation into two kinds of tissue. Note the numerous crystals of calcium oxalate in the larger cells. Partly camera lucida, x 60.

FIGURE XXII.



a



b

Fig. XXIII . Transverse section of the pith of R. longistylum, taken immediately below the apical bud, and showing an unusual development of sclereids. Camera lucida, x 250.

FIGURE XXIII.

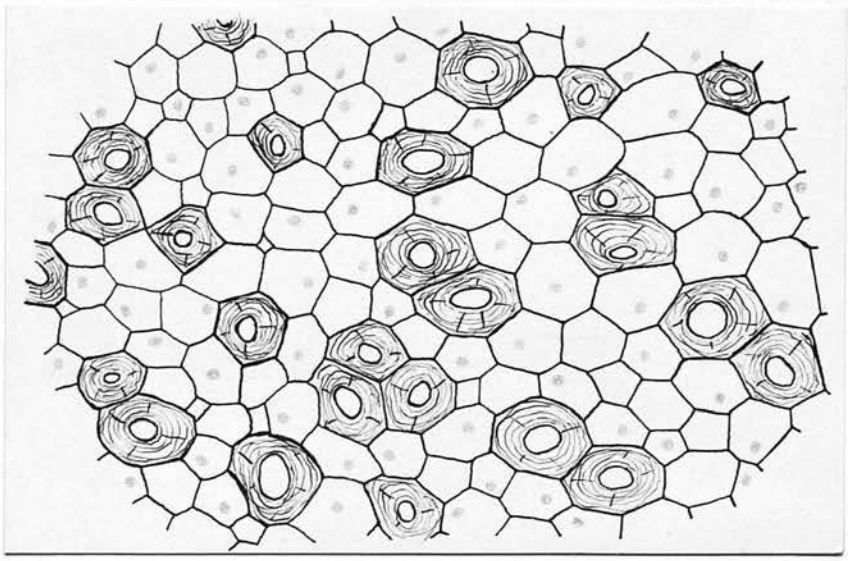


Fig. XXIV . Transverse section of the outer portion of the stem of R. serpyllifolium showing a uniform and extremely narrow cortex, a considerable development of pericyclic fibres, and a phellogen internal to the pericycle. c = cortex, f = pericyclic fibres, v = phellogen, p = phloem.

Cam. luc.

FIGURE XXIV.

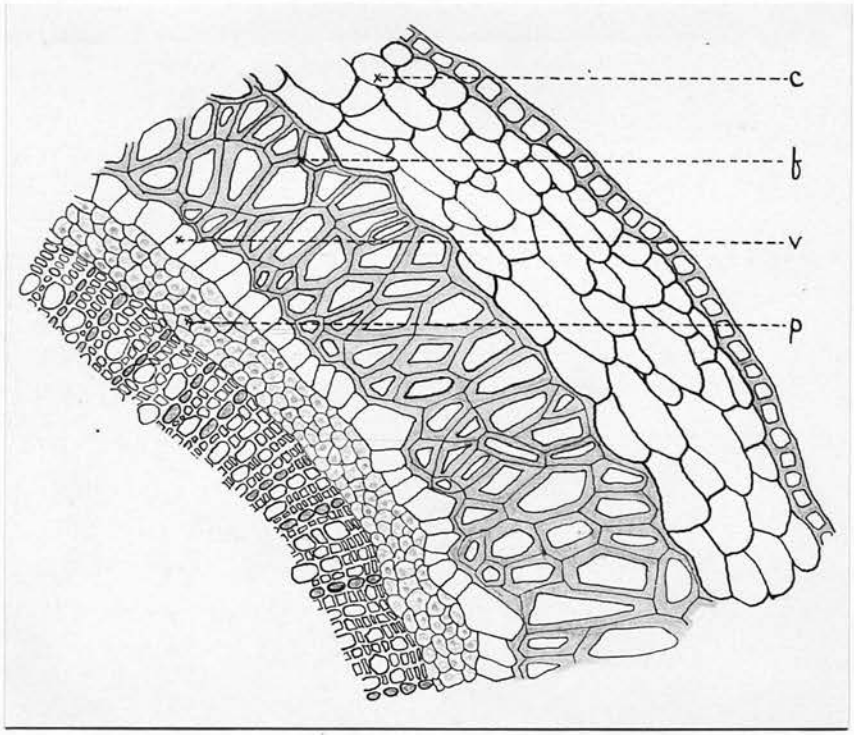


Fig.XXV . Transverse section of the outer portion of a young stem of R. primulinum, showing slight differentiation of tissue and abundant large sclereids in the cortex. Note the roughened cuticle and numerous epidermal hairs. s = sclereid, f = pericyclic fibres, p = phloem. Camera lucida, x 270.

FIGURE XXV.

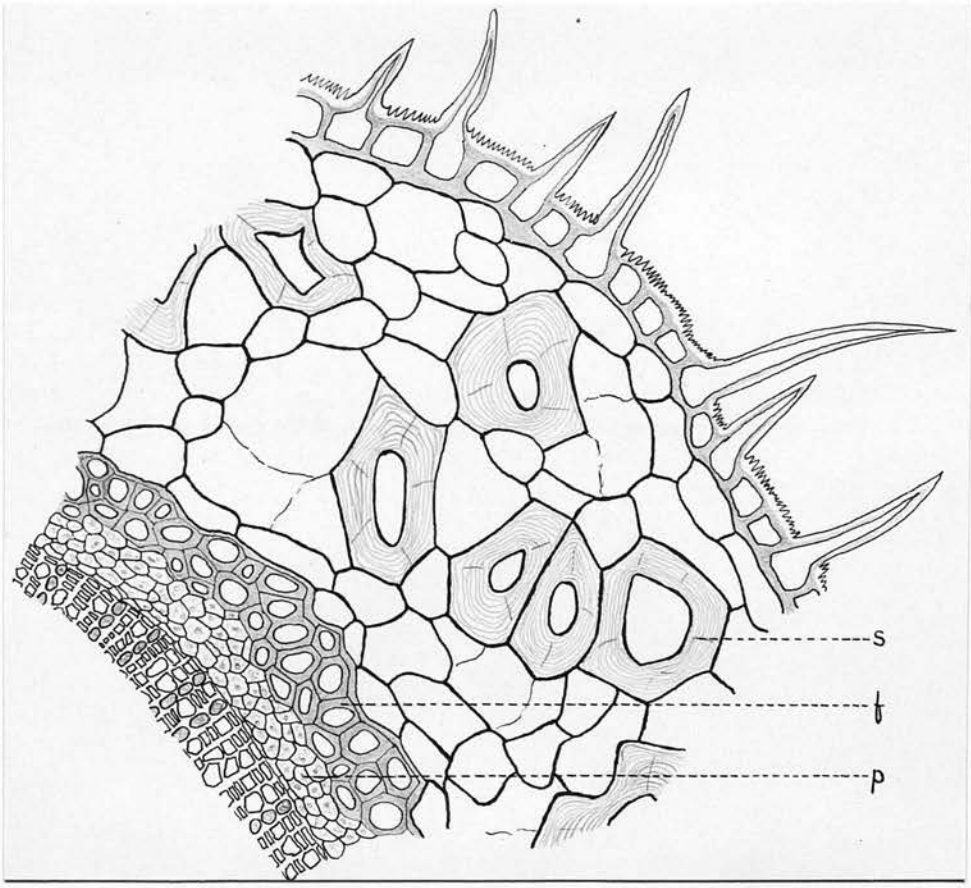
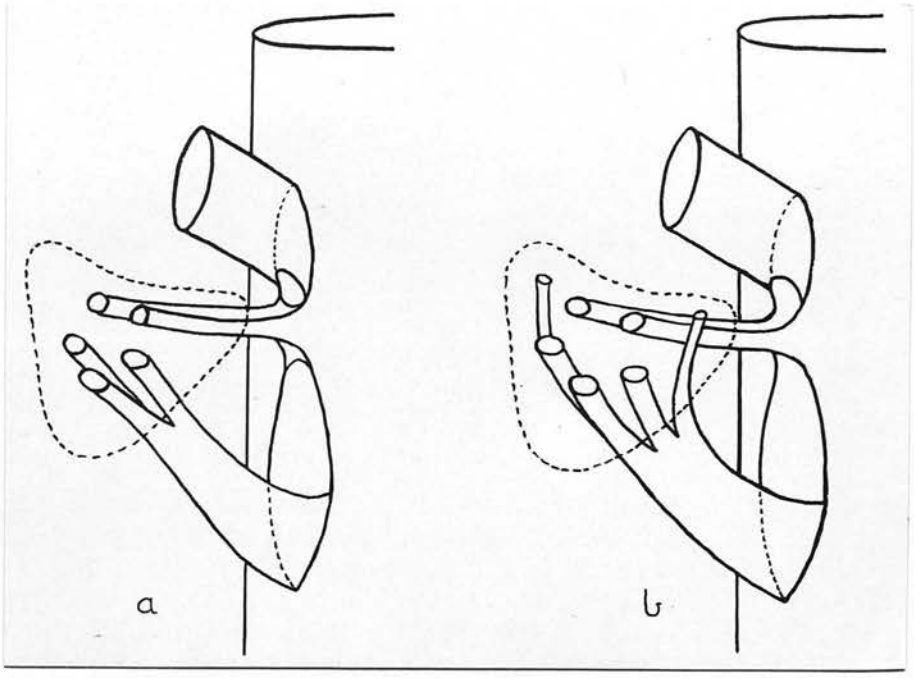


Fig. XXVI. Diagrams illustrating variations in nodal anatomy of Rhododendron, and representing the junction of the leaf-traces with the main vascular cylinder. Position of leaf-scar indicated in dotted lines, bud axis immediately above. (a) leaf-trace of five strands, fusing normally with the main stele, (b) seven strands, the outermost pair fusing with the three lower strands, (c) seven strands, the uppermost pair fusing with the bud-trace, (d) five strands, the outermost pair remaining separate and fusing with the main cylinder at varying positions. (a) and (c) show the closing of the vascular cylinder between bud- and leaf-trace.

FIGURE XXVI.



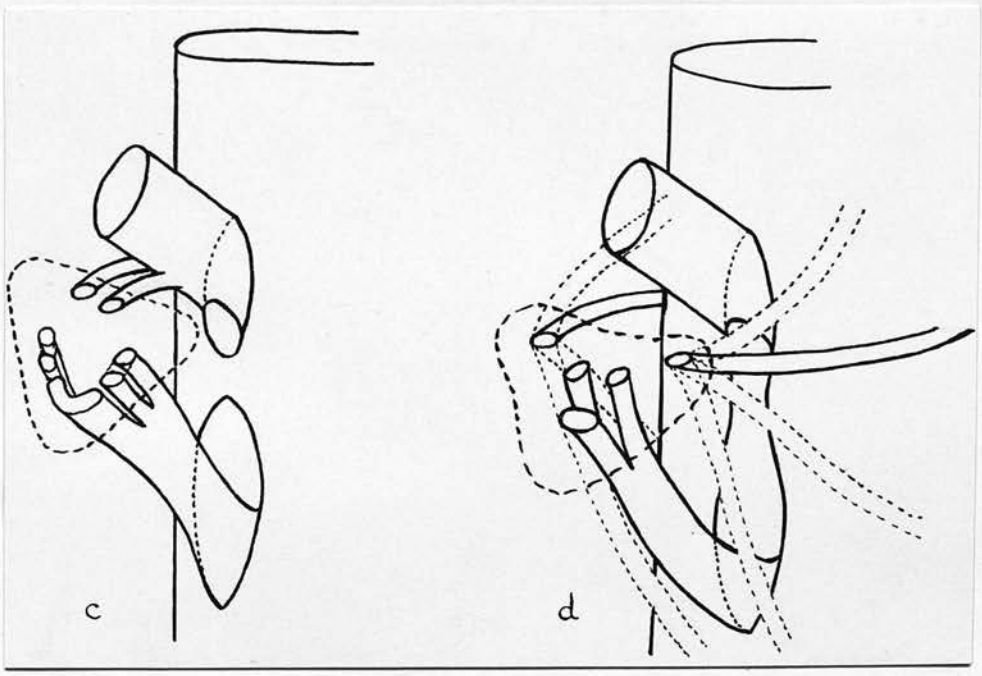


Fig. XXVII. Transverse section of R. Griffithianum across a node, showing the leaf-base cut obliquely: (a) shows the three central strands fused, and the two outer strands entering to join the main vascular cylinder, (b) the outer strands have fused with the main cylinder, (c) the two upper central strands have fused with the main cylinder, and the fused lower central ones are entering in.

FIGURE XXVII.

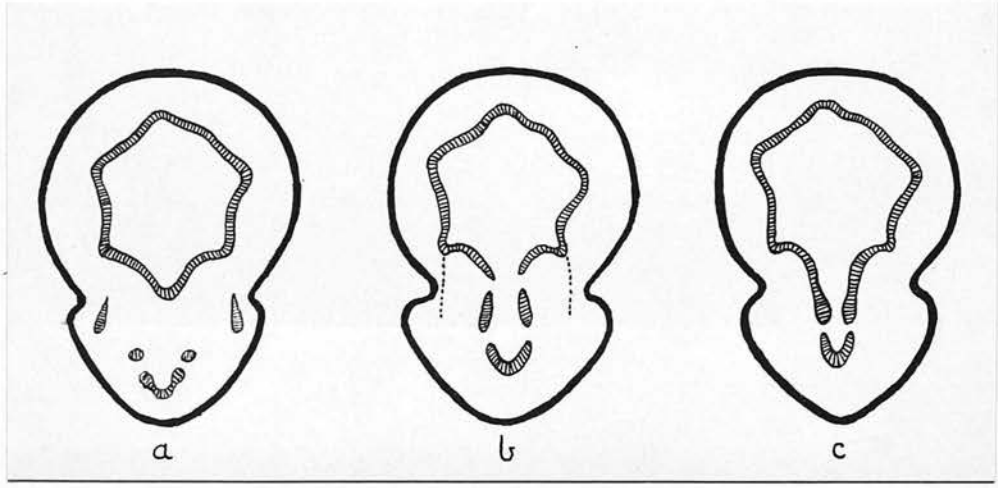
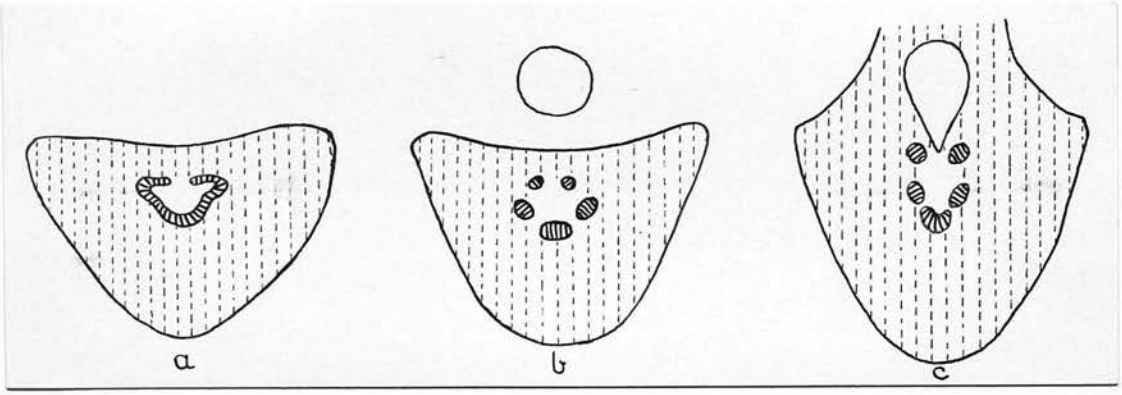


Fig. XXVIII. Diagrams representing serial sections from a leaf-base to the vascular cylinder of the stem: (a) transverse section through petiole showing one petiolar trace, (b) leaf scar showing five separate traces: axillary bud axis immediately above, (c) vertical section taken immediately within the axillary bud and leaf-scar, (d) vertical section through the outer cortex showing fusion of three lower strands and union of the upper two with the vascular supply of the bud, (e) through the central cortex showing complete fusion of leaf-traces with axillary bud cylinder, (f) through the wood cylinder showing fusion of bud- and leaf-traces with the main vascular supply.

FIGURE XXVIII.



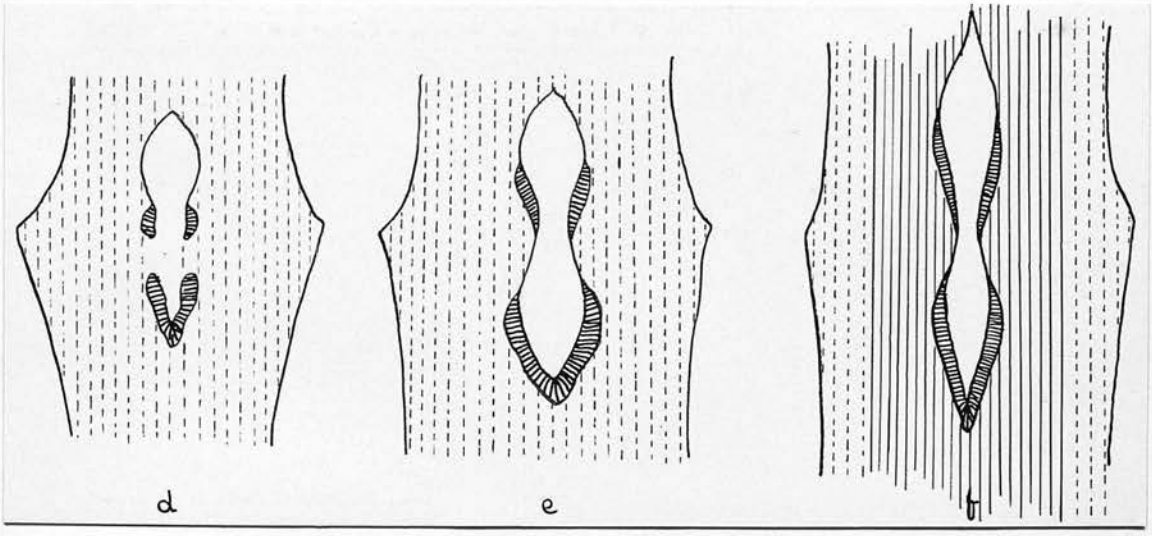


Fig. XXIX. Two kinds of multiseriate unbranched hairs from the upper surfaces of leaves of (a) R. pendulum, (b) R. obtusum. Camera lucida, x 270.

FIGURE XXIX.

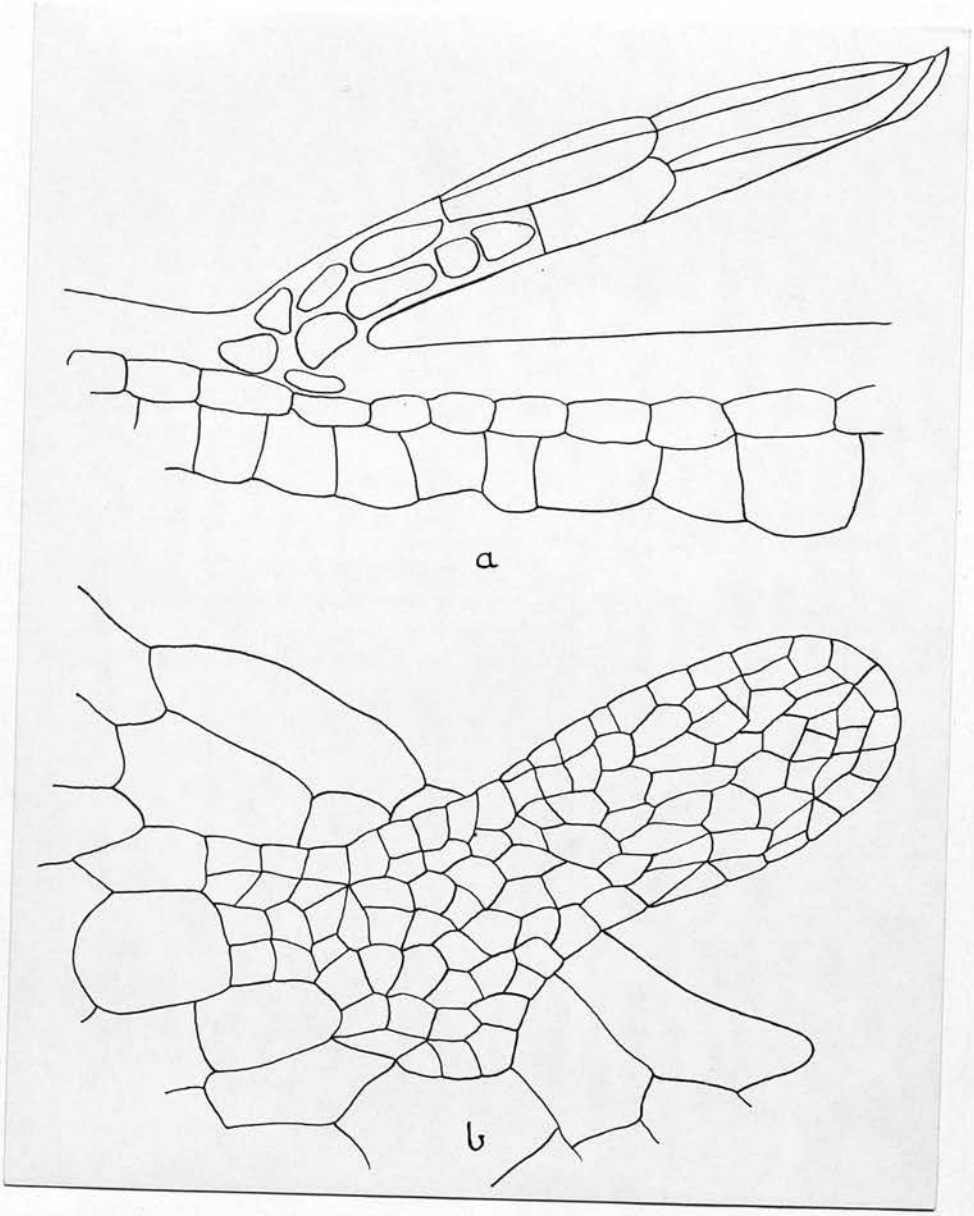


Fig. XXX. Four kinds of multiseriate unbranched hairs from the leaves of (a) R. bullatum, (b) R. callimorphum (petiole), (c) R. austrinum, (d) R. schistocalyx (petiole). Camera lucida x 60.

FIGURE XXX.

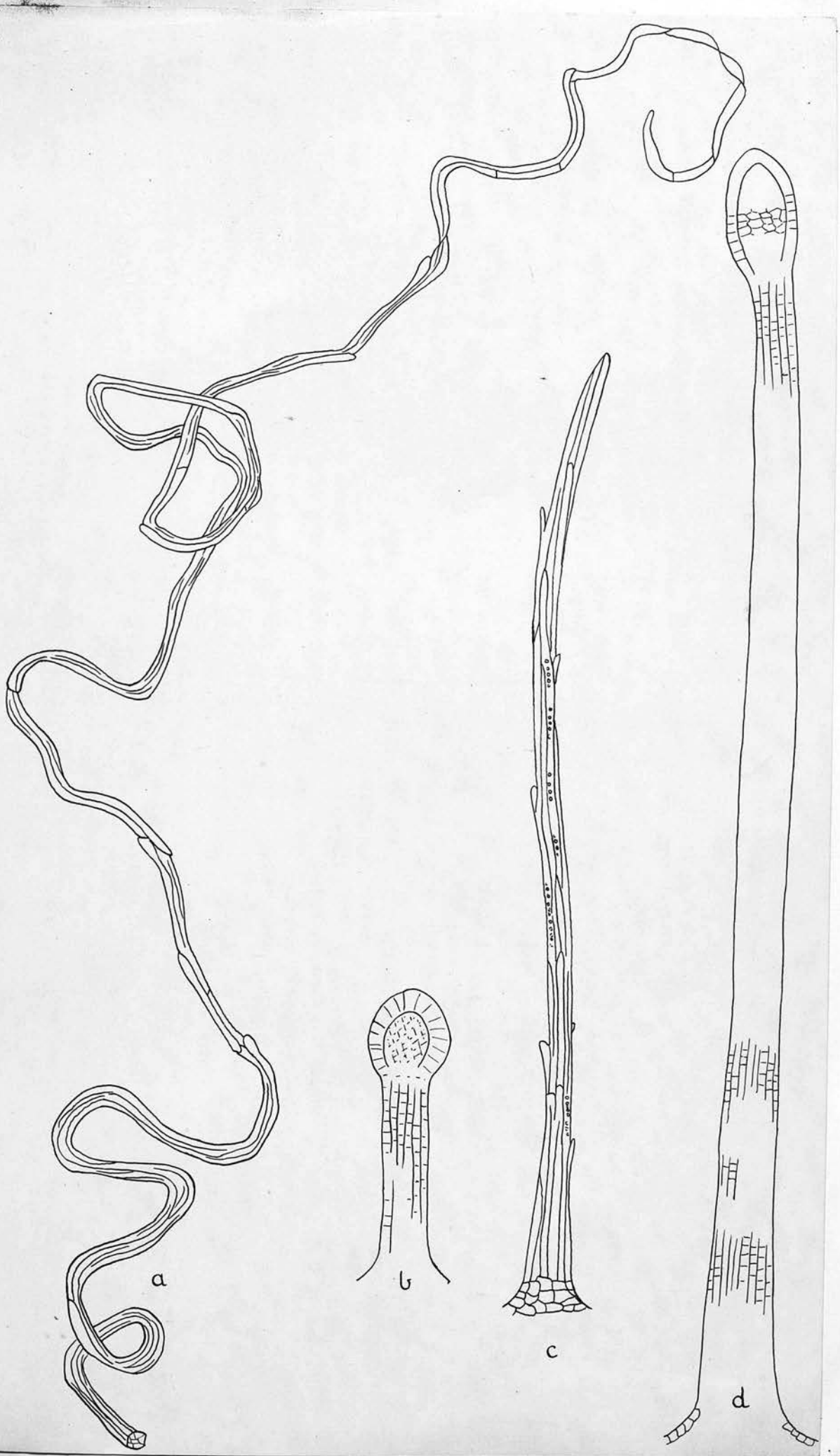


Fig. XXXI. Three kinds of multiseriate branched hairs from leaves of (a) R. Hookeri, (b) R. prophantum, (c) R. aemulorum. Camera lucida, x 60.

FIGURE XXXI.

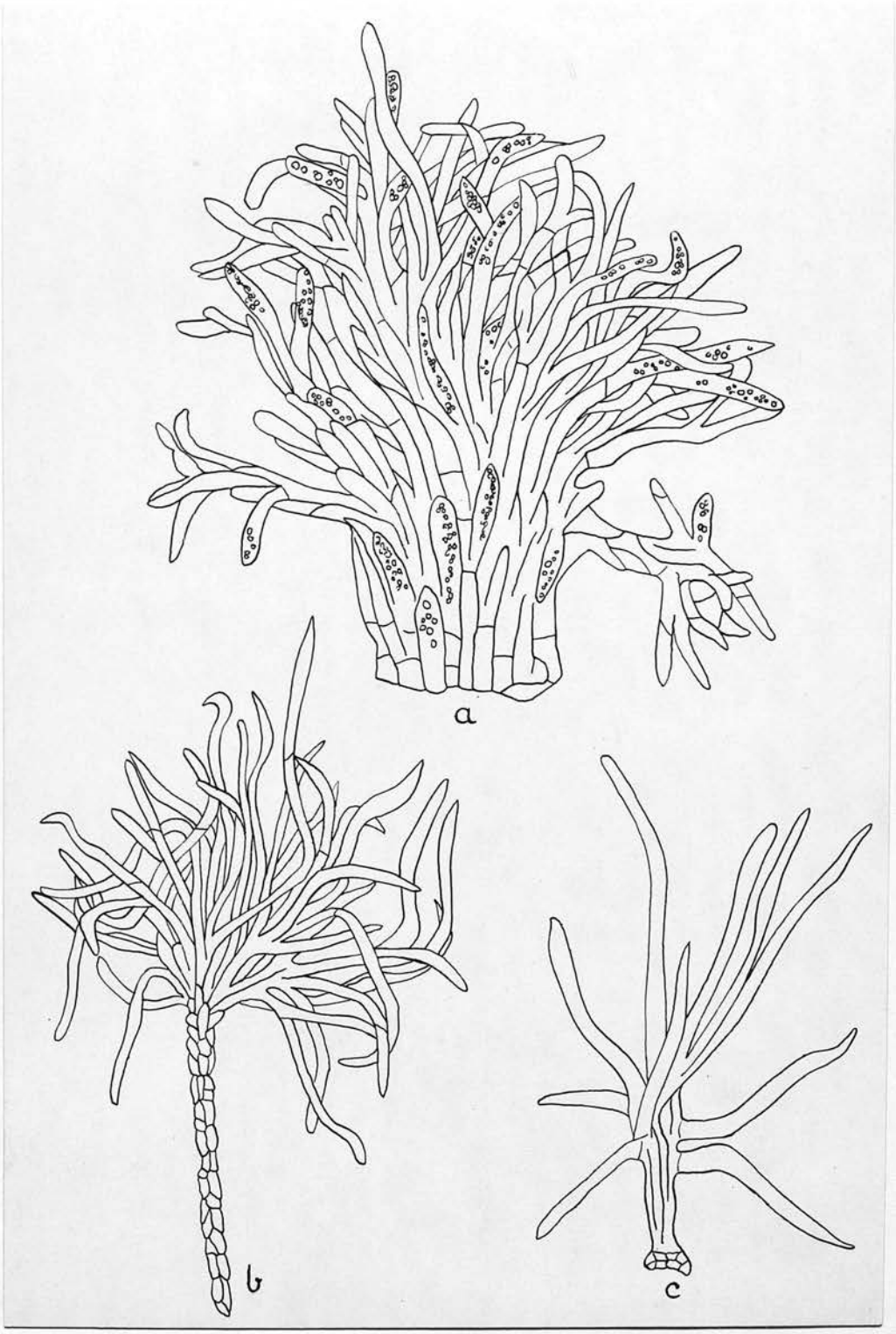


Fig. XXXII. Hairs from the lower surfaces of leaves of (a) R. Falconeri, side view, (b) R. Hodgsoni, side view, (c) R.fictolacteum, surface view. Camera lucida X 60.

FIGURE XXXII.

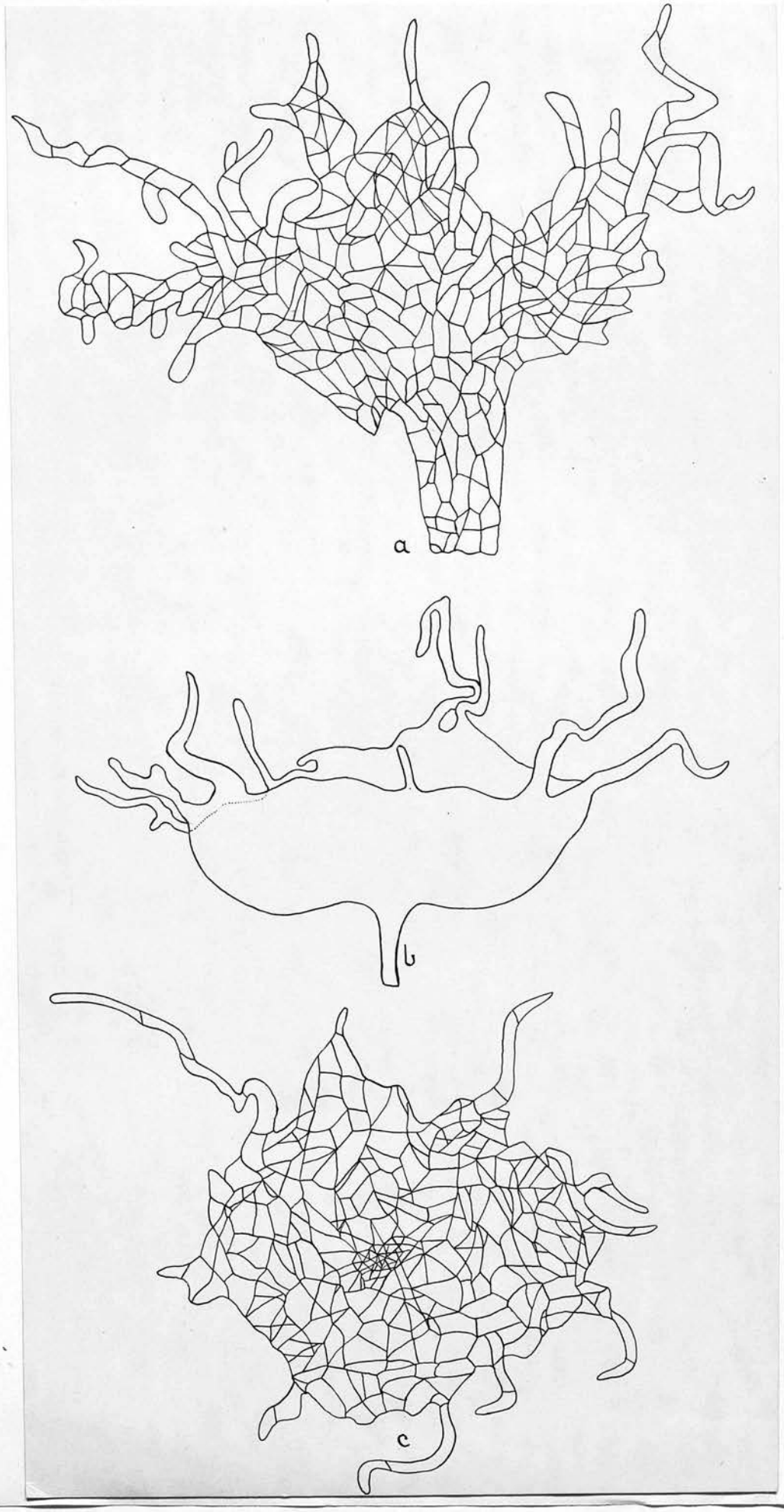


Fig. XXXIII. Types of leaf-hairs: (a) from R. camelliaeflorum, surface view, (b) from R. pendulum, surface view, (c) from R. primulinum, vertical section, (d) from R. anthopogon surface view, (e) from R. arboreum, surface view, (f) from R. fulvum, surface and side view.

FIGURE XXXIII.

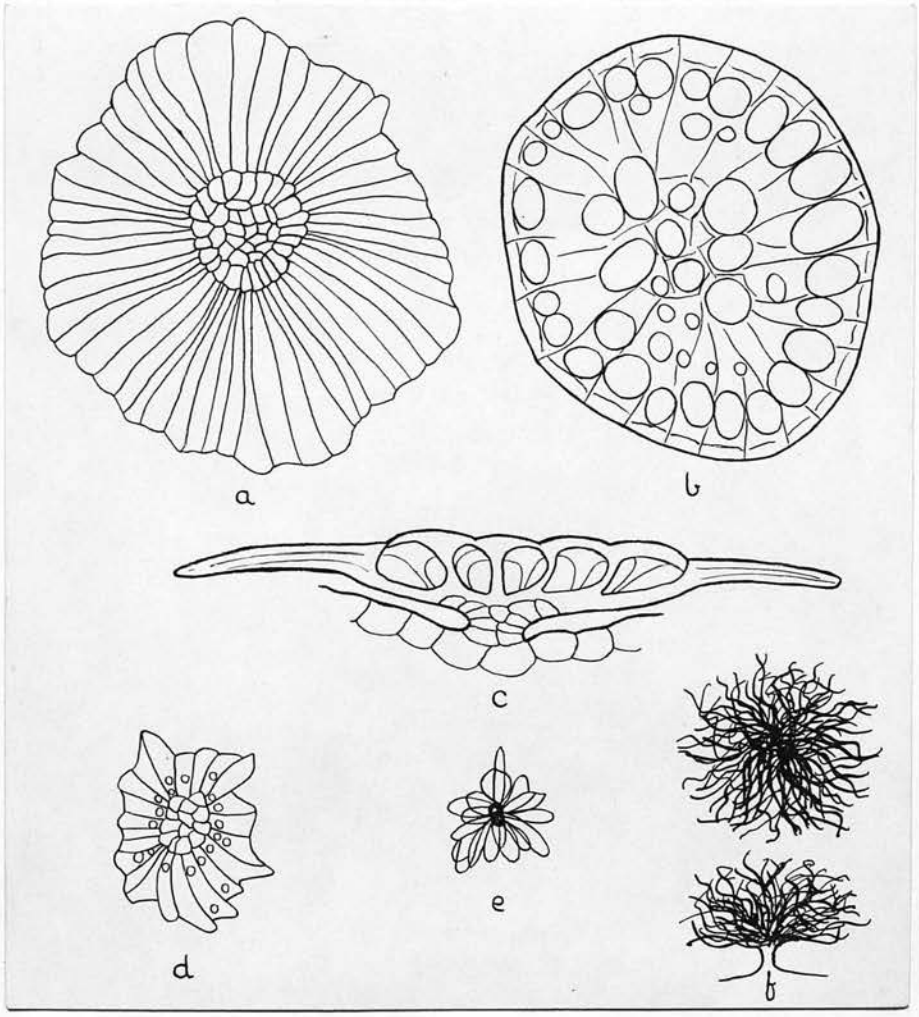
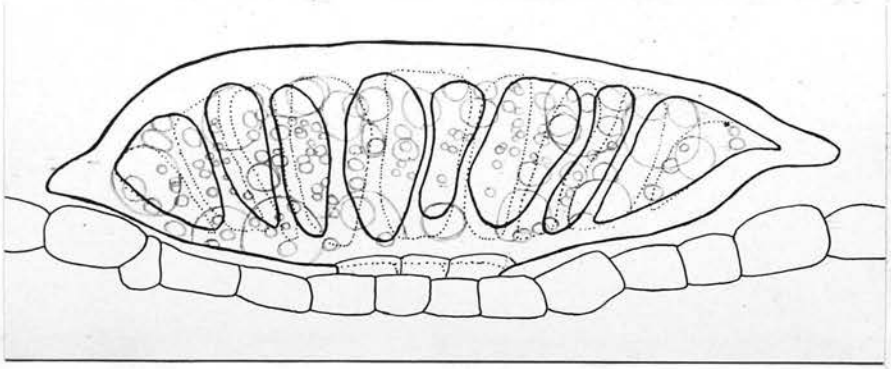
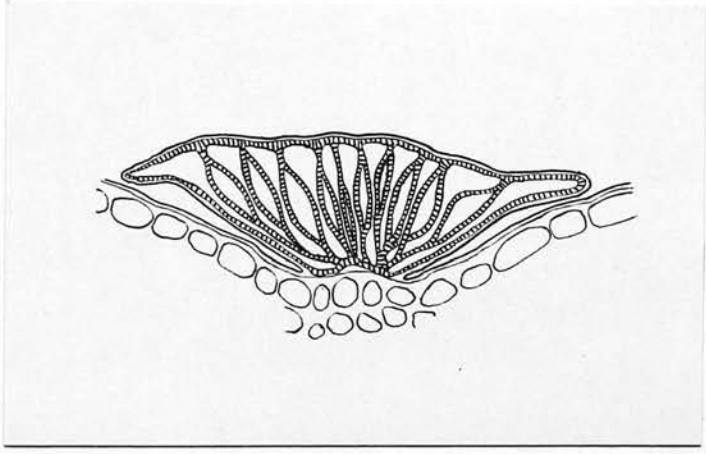


Fig. XXXIV. Three hairs from the leaf of R. hirsutum seen in vertical section showing highly developed central mass and small ray cells: (a) containing abundant oil droplets. (a) and (c) camera lucida x 270: (b) after De Bary, x 225.

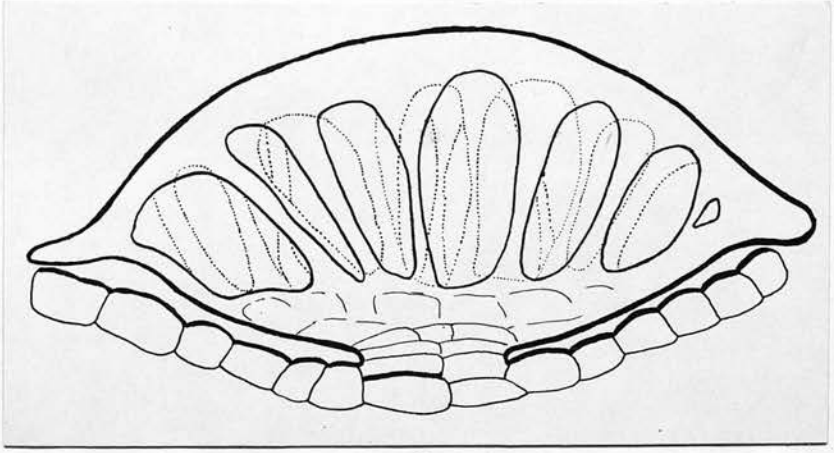
FIGURE XXXIV.



a



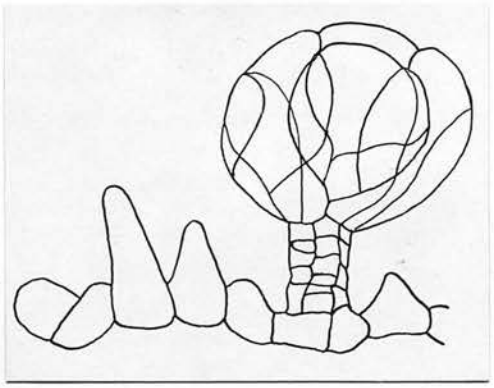
b

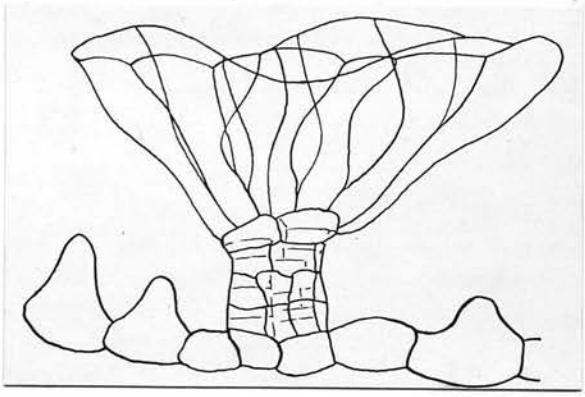


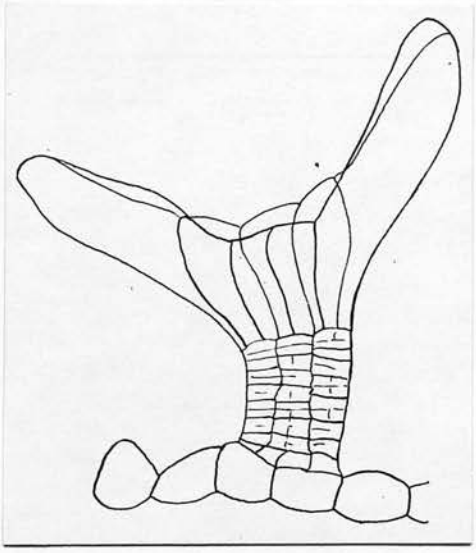
c

Fig. XXXV. Four stages in the development of a hair from the leaf of R. anthopogon. Camera lucida, x 270.

FIGURE XXXV.







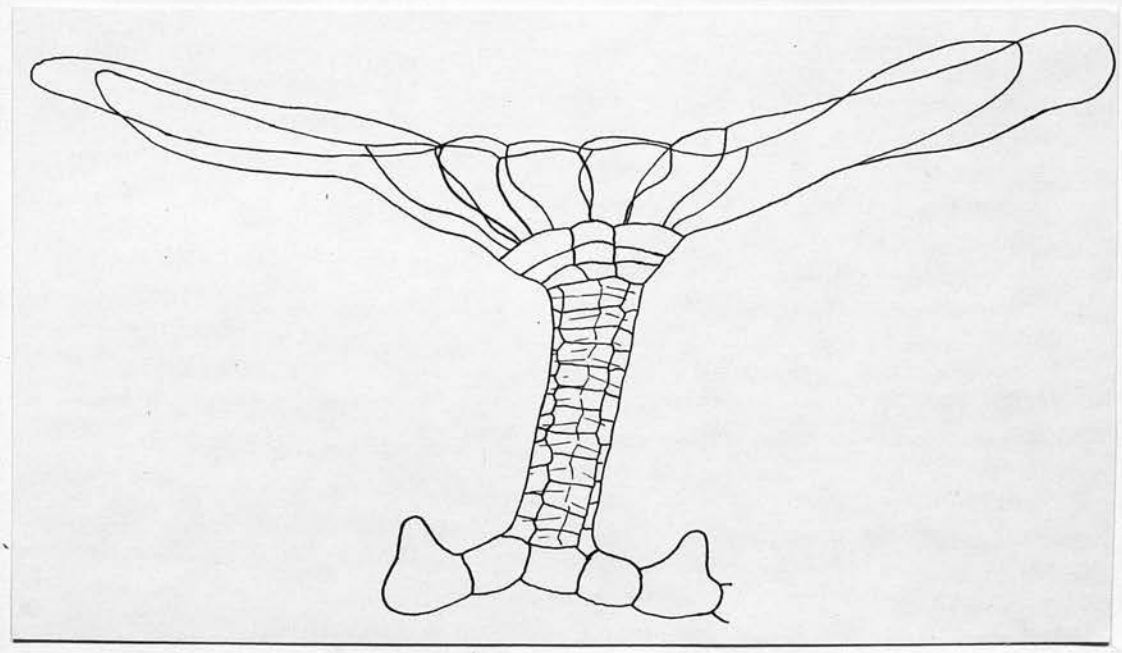


Fig. XXXVI. Two hairs from the lower surface of the leaf of R. pendulum, one in vertical section: s = stoma, p = epidermal papilla.

FIGURE XXXVI.

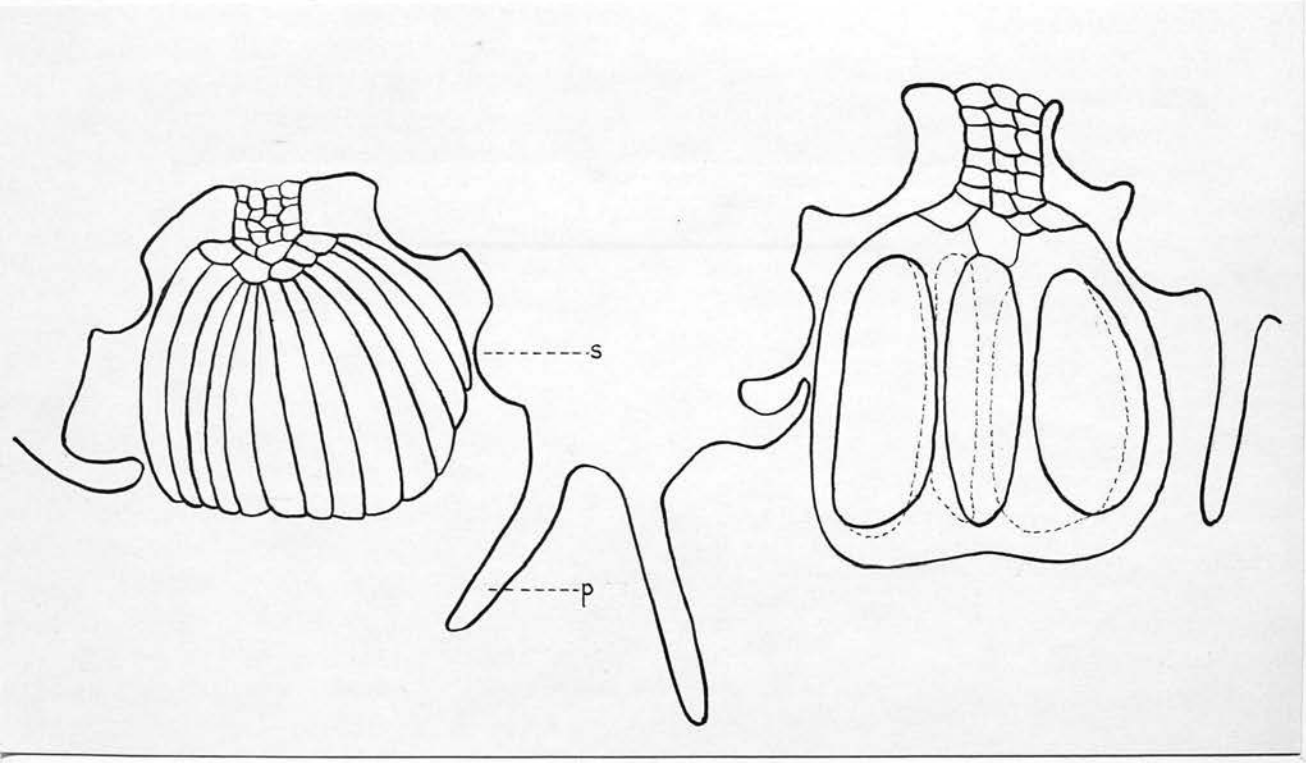
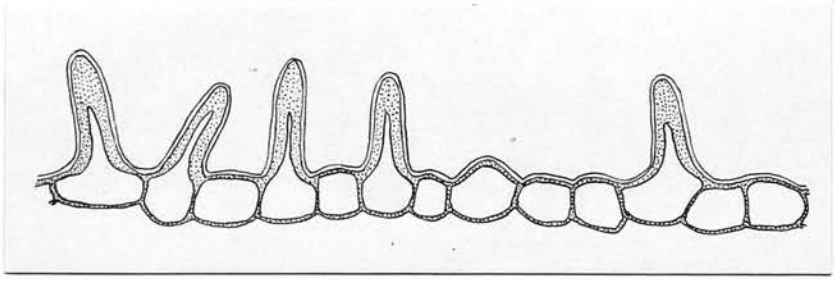


Fig. XXXVII. Transverse section of some epidermal cells from the leaf of (a) R.triflorum (b) R. pendulum, showing papillose structure. x 279.

FIGURE XXXVII.



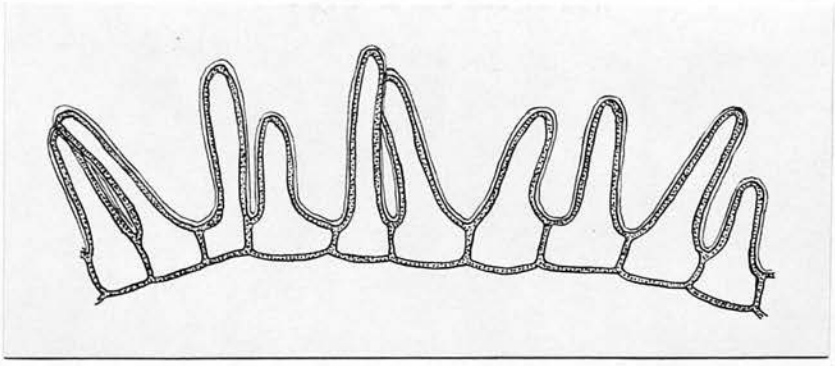


Fig. XXXVIII. Transverse section of midribs of (a) R. floribundum, (b) R. decorum showing median vascular bundles. Phloem in black, sclerenchyma stippled. Camera lucida X 30.

FIGURE XXXVIII.

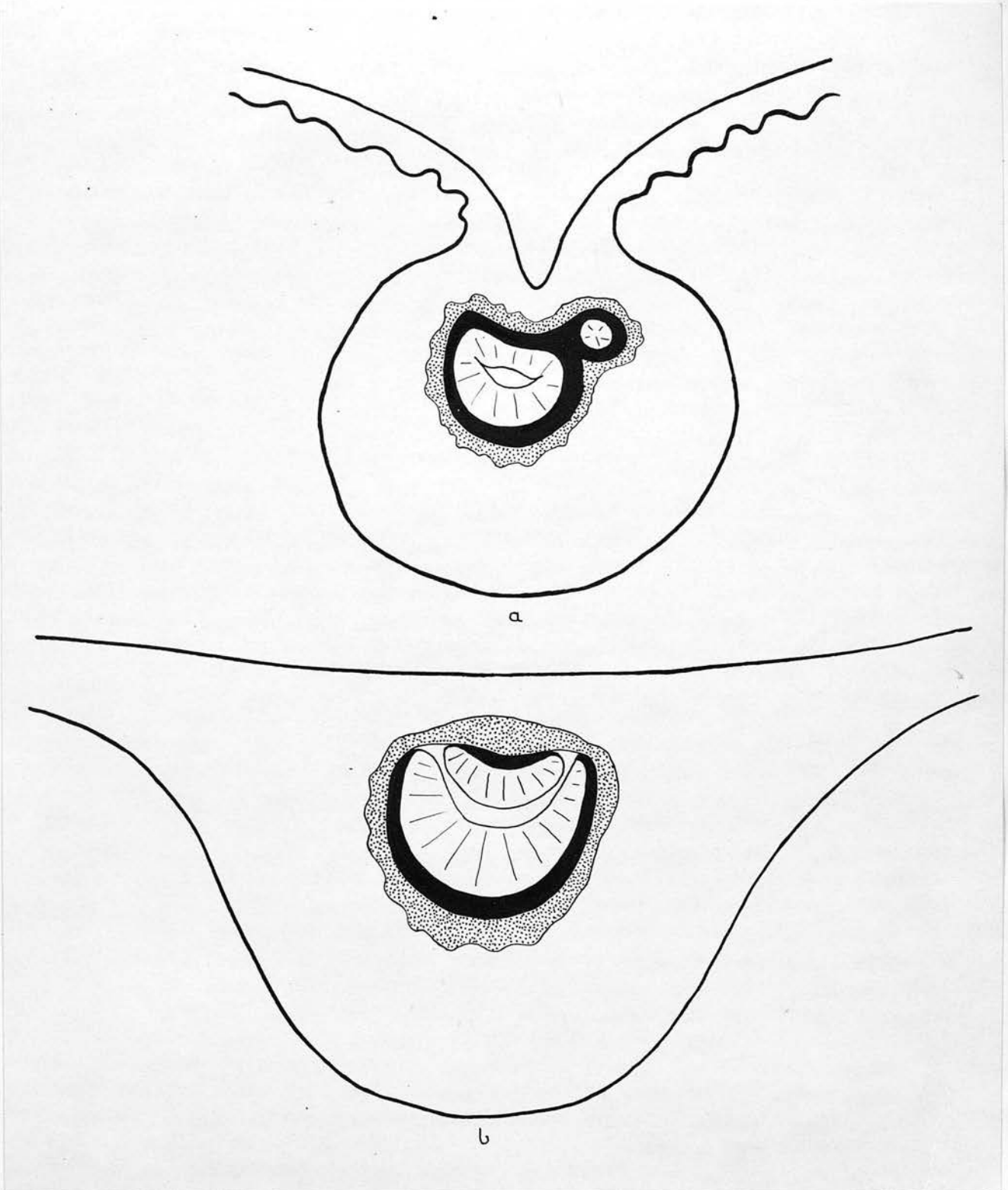


Fig. XXXIX. Portion of the lower epidermis surrounding a peltate hair (which has been removed), from the leaf of R. ciliicalyx showing localisation of the stomata. Note the large area occupied by the hair, and the epidermal papillae (seen in surface view) arising from the centre of each cell. Camera lucida, x 150.

FIGURE XXXIX.

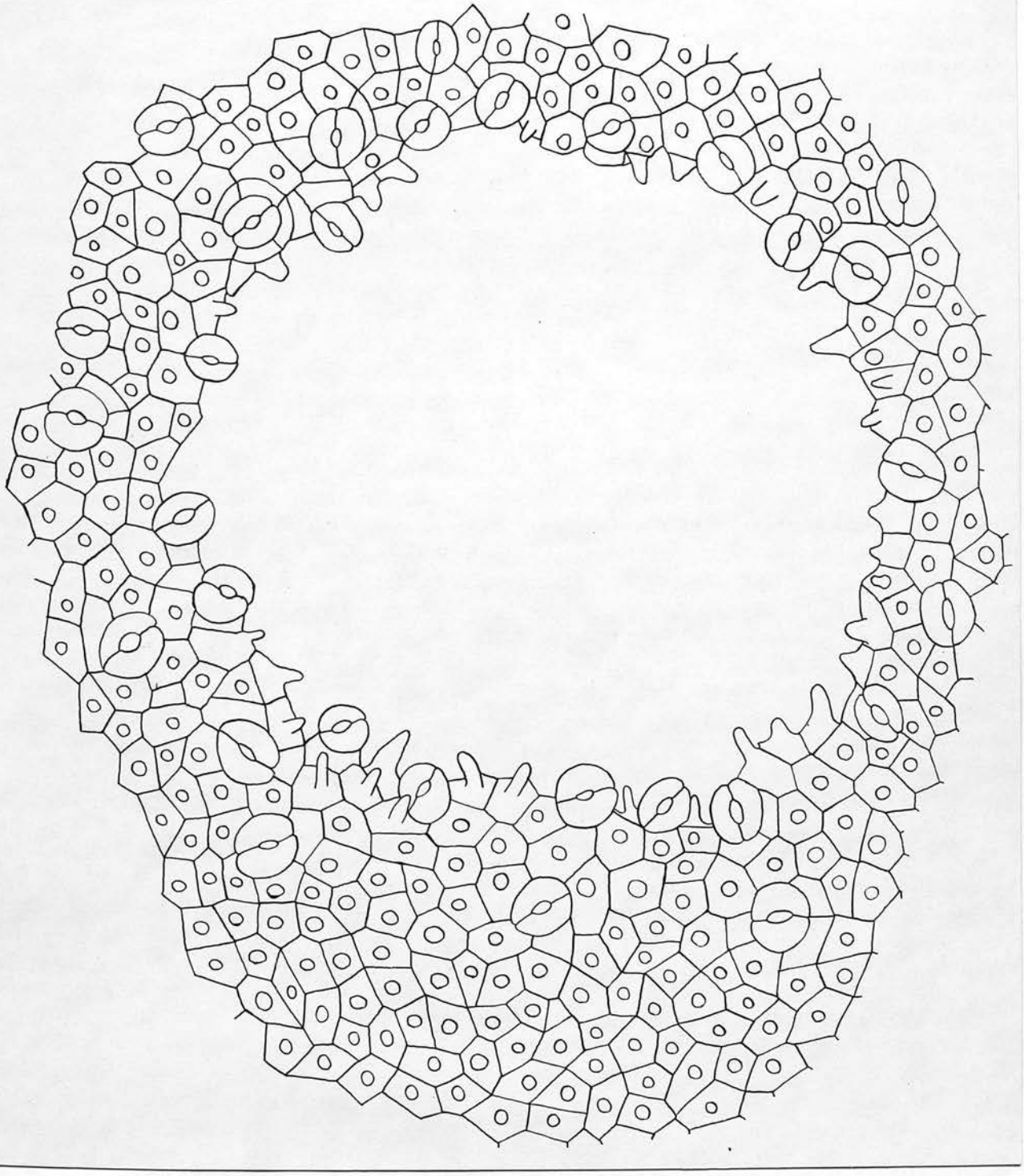
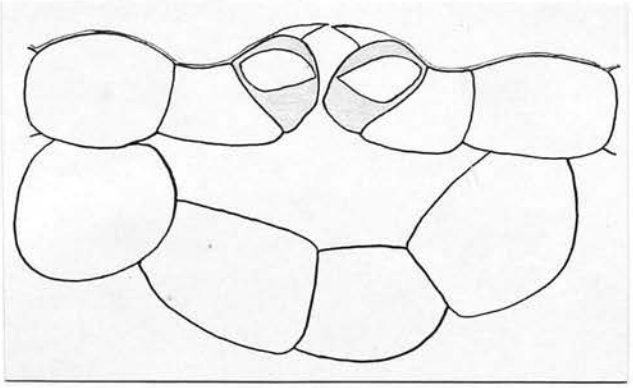
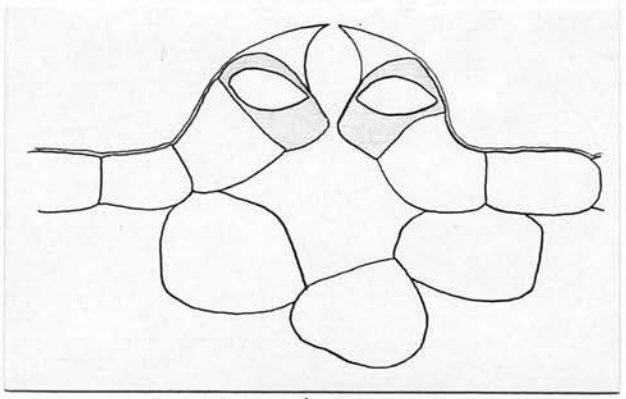


Fig. XL. Stomata, in vertical section, from the leaves of: (a) R. serpyllifolium, (b) R. triflorum, (c) R. fulgens, (d) R. argenteum. Camera lucida, x 660.

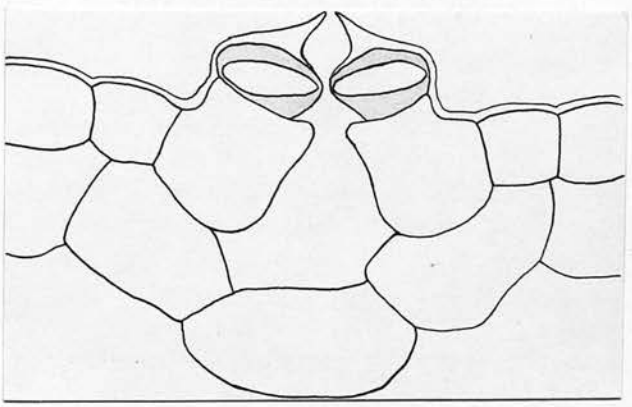
FIGURE XL.



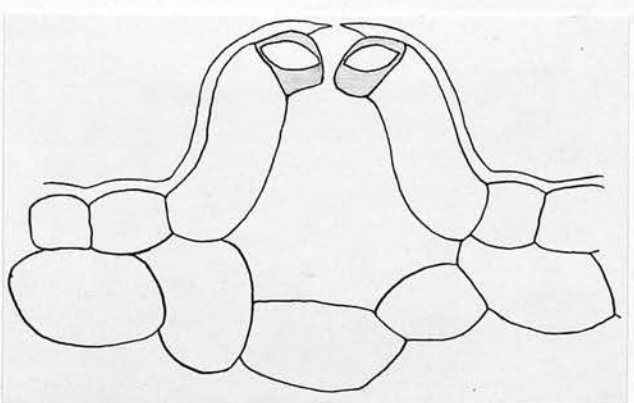
a



b



c



d

Fig. XLI . Surface view of a portion of the lower epidermis of R. obtusum, showing stomata level with the epidermis. Note the shape of the adjacent epidermal cells and their straight walls, in contrast to the sinuous walls of the surrounding cells. Camera lucida, x 500.

FIGURE XLI.

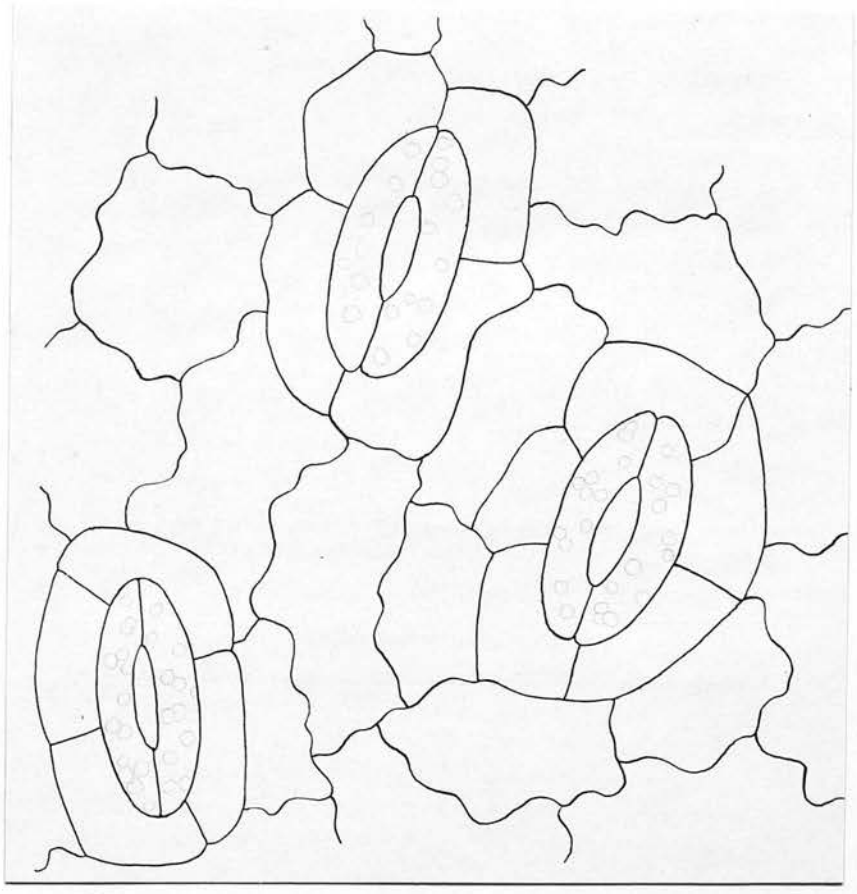
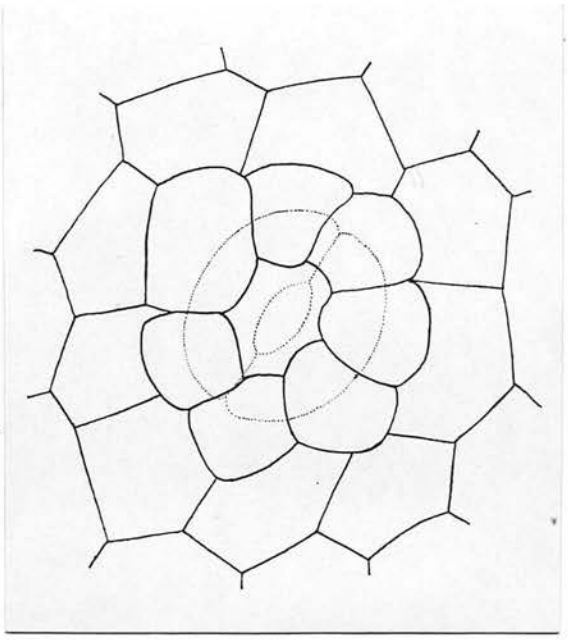
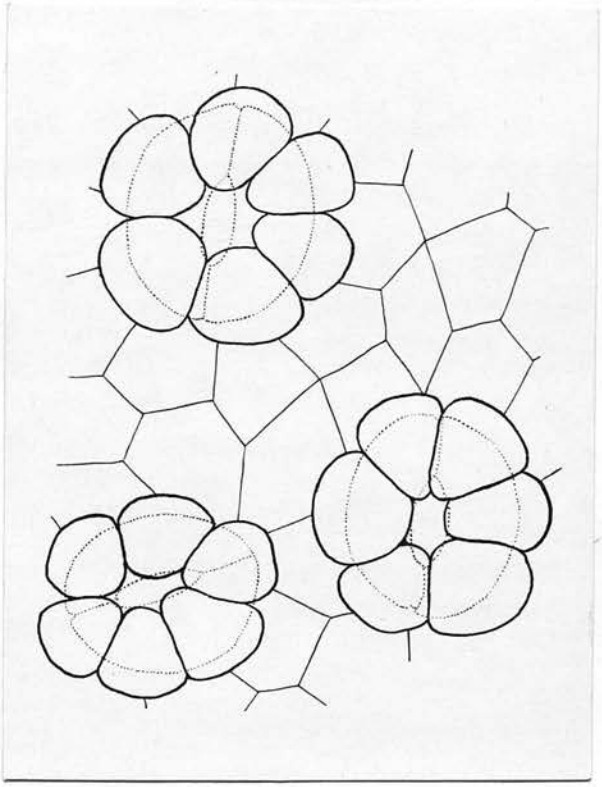


Fig. XLII. Surface view of a few lower epidermal cells from the leaf of (a) R. fulgens, (b) R. arboreum, showing stomata. (a) all epidermal cells in focus, guard-cells above plane of focus, (b) adjacent epidermal cells in focus, guard-cells above , normal epidermal cells below plane of focus. Camera lucida X 500.

FIGURE XLII.



a



b

Fig.XLIII . Transverse section through part of a leaf of R. primulinum showing small, thick-walled upper epidermal cells, and short palisade cells. Camera lucida, x 150.

FIGURE XLIII.

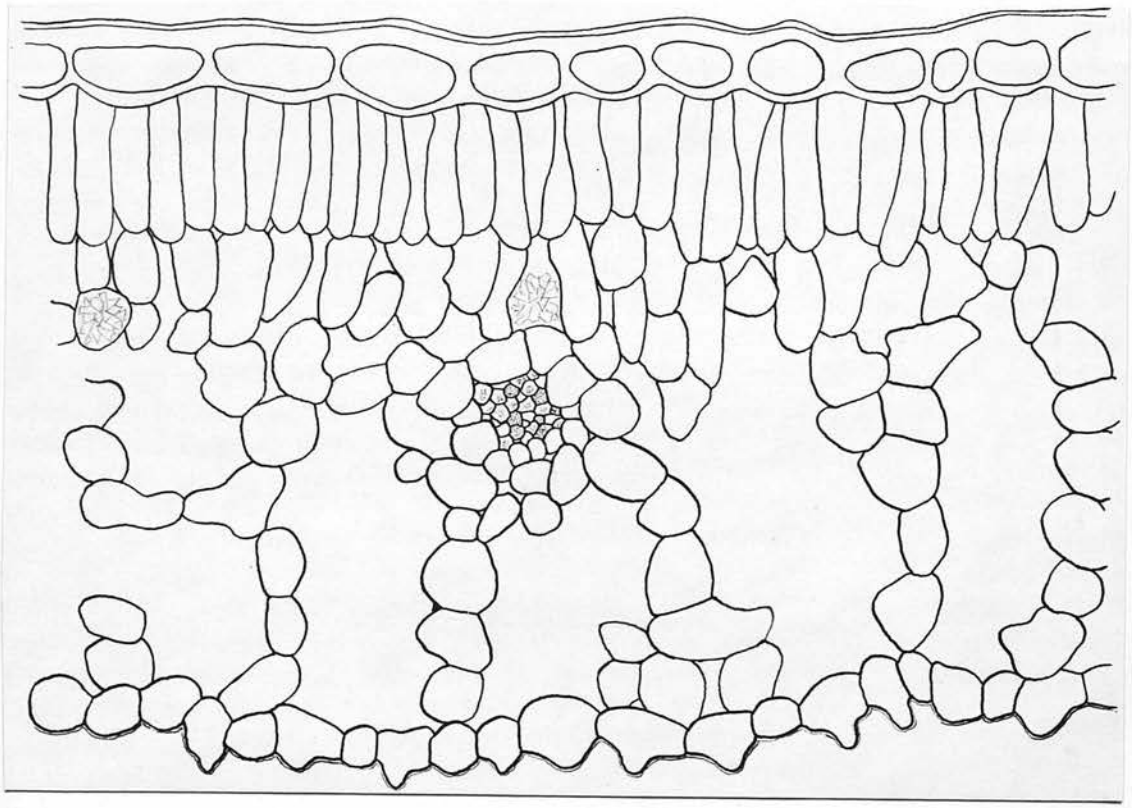


Fig. XLIV. Transverse section through the leaf of R. Weyrichii showing unusual depth of lamina and very large upper epidermal cells. Camera lucida, x 270.

FIGURE XLIV.

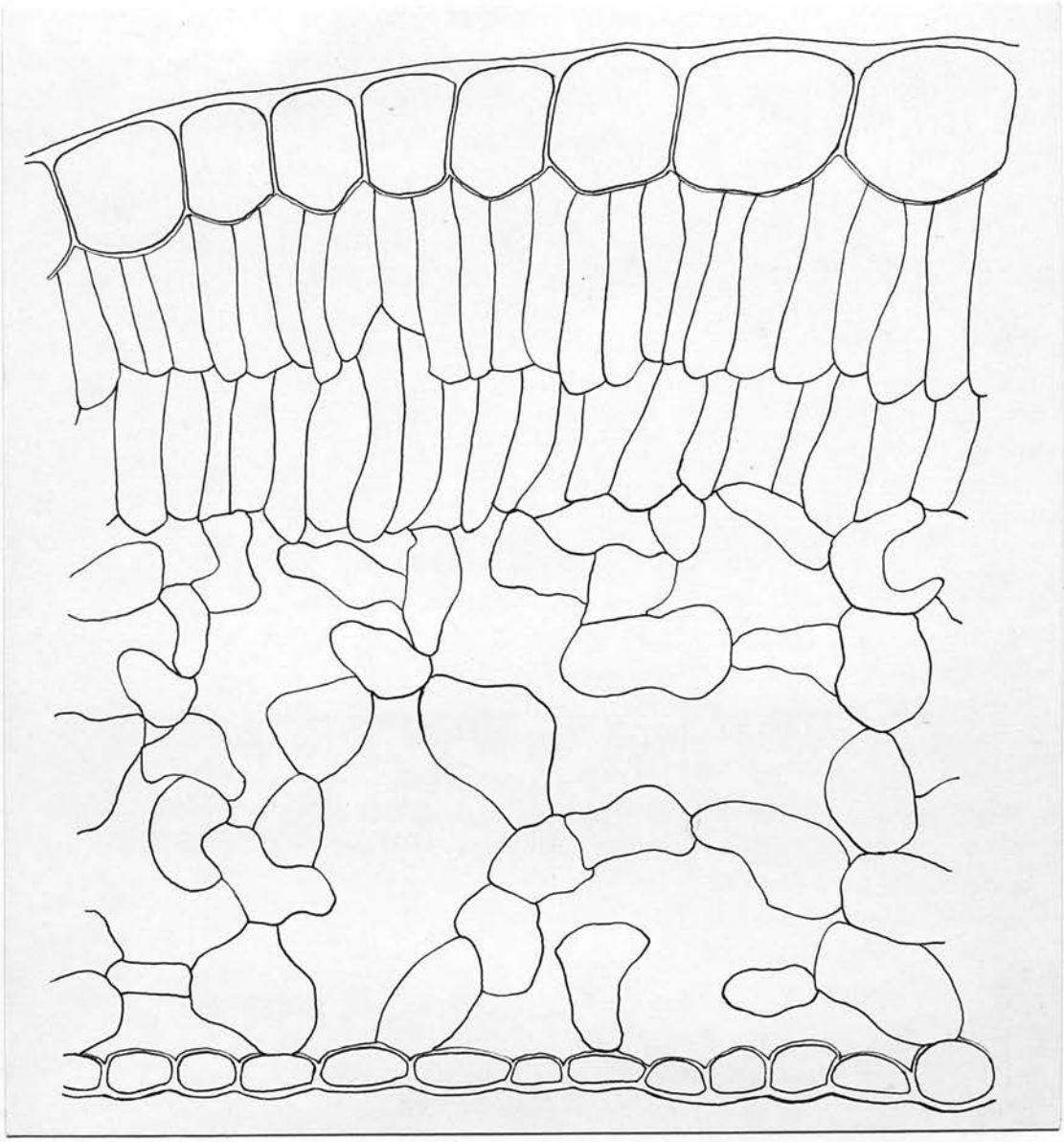


Fig. XLV . Transverse section through part of a leaf of R. Davidii showing a thick-walled hypodermis and elongated palisade cells. Camera lucida x 150.

FIGURE XLV.

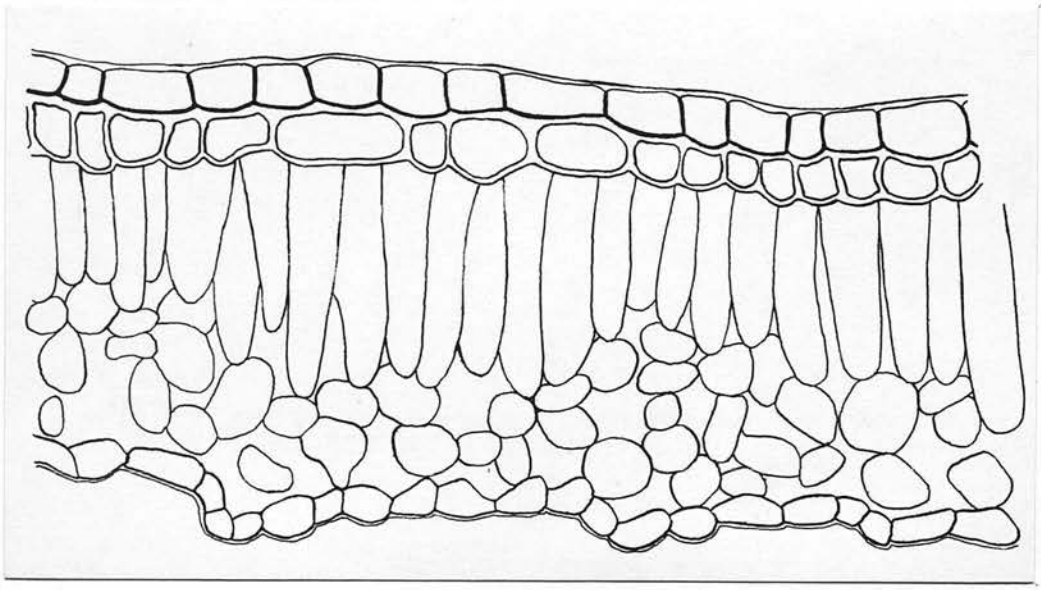


Fig. XLVI . Transverse section of the upper part of a leaf of R. pendulum showing very thick cuticle, and enlarged pitted hypodermal cells. Camera lucida, x 270.

FIGURE XLVI.

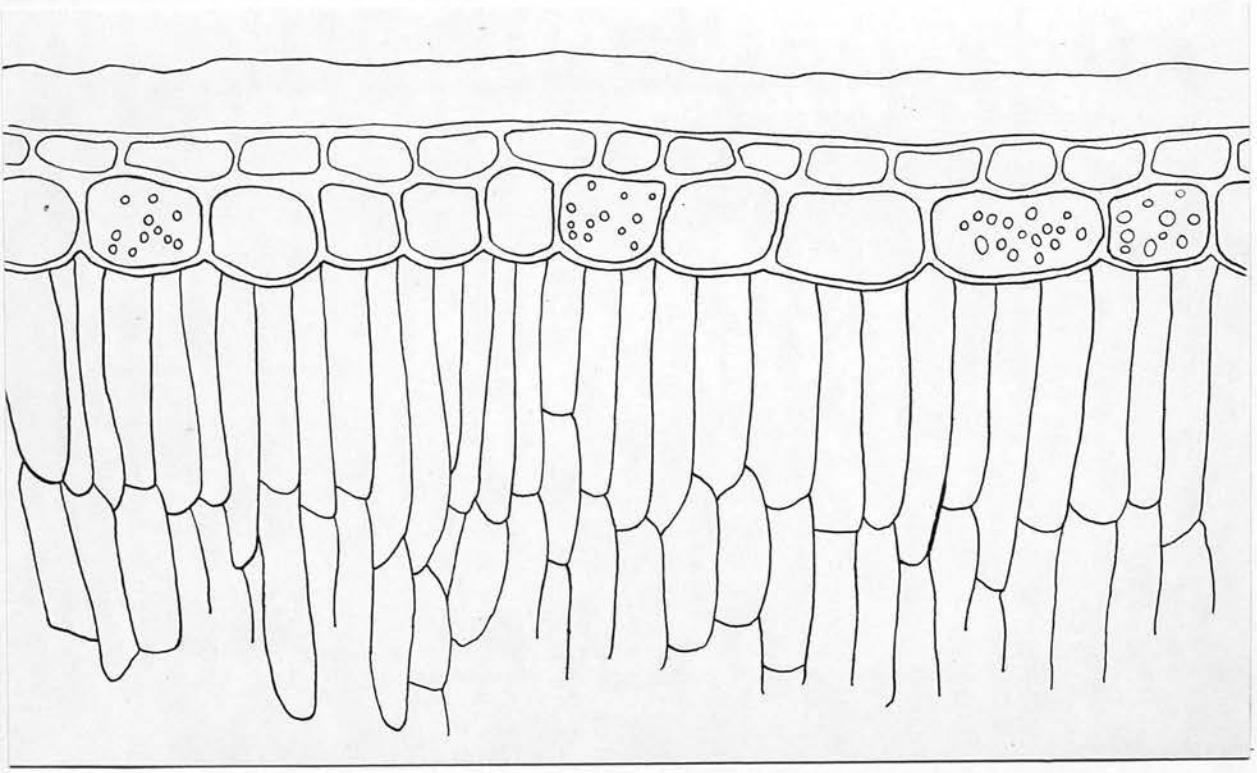


Fig. XLVII . Transverse section of the upper portion of a leaf of R. javanicum showing enlarged hypodermal cells. Camera lucida, x 270.

FIGURE XLVII.

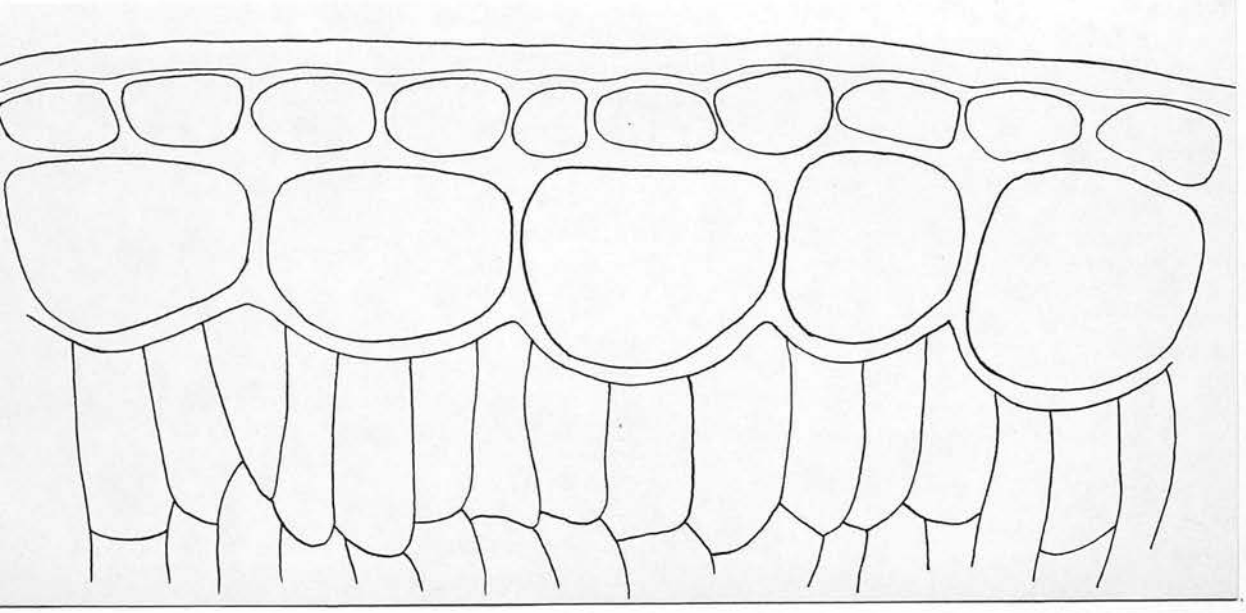


Fig. XLVIII . Transverse section of the upper part of a leaf of R. retusum, showing greatly enlarged hypodermal cells. Camera lucida, x 270.

FIGURE XLVIII.

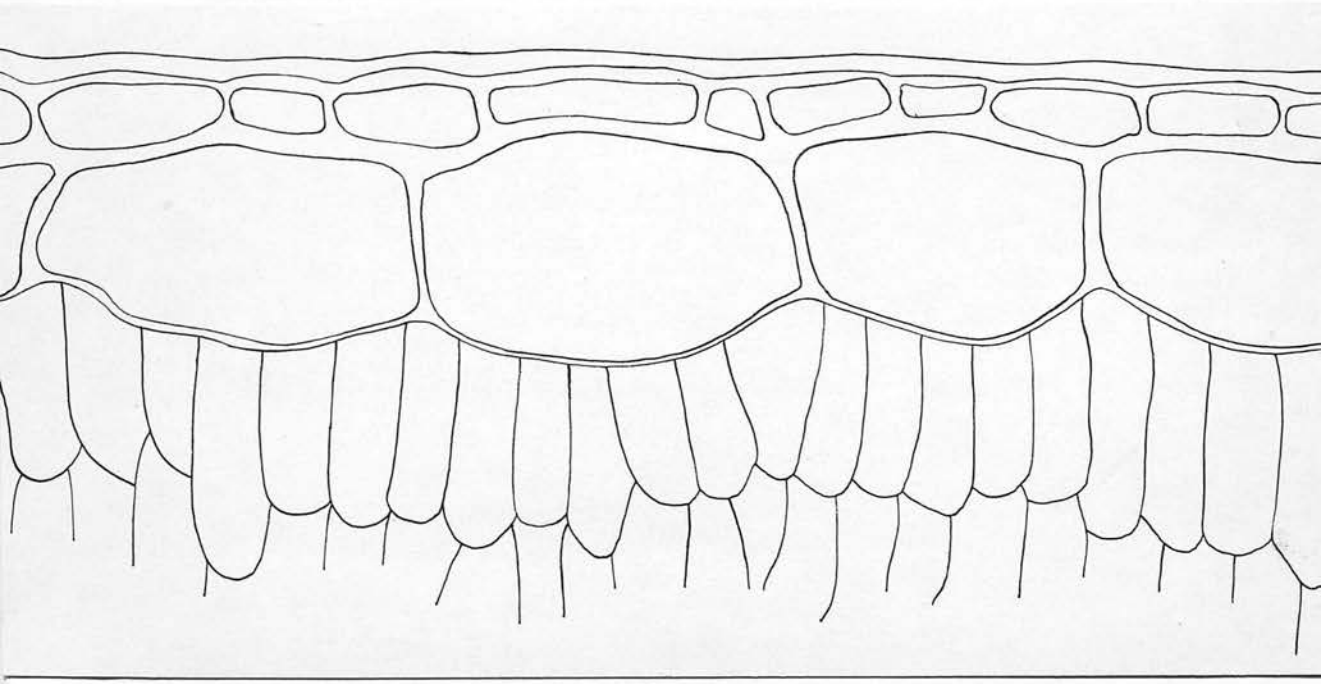


Fig. XLIX. Transverse section through part of a leaf of Rhododendron hybrid (javanicum x) showing much enlarged hypoderm cells on both surfaces, these and the epidermal cells containing oil droplets. Camera lucida X 270.

FIGURE XLIX.

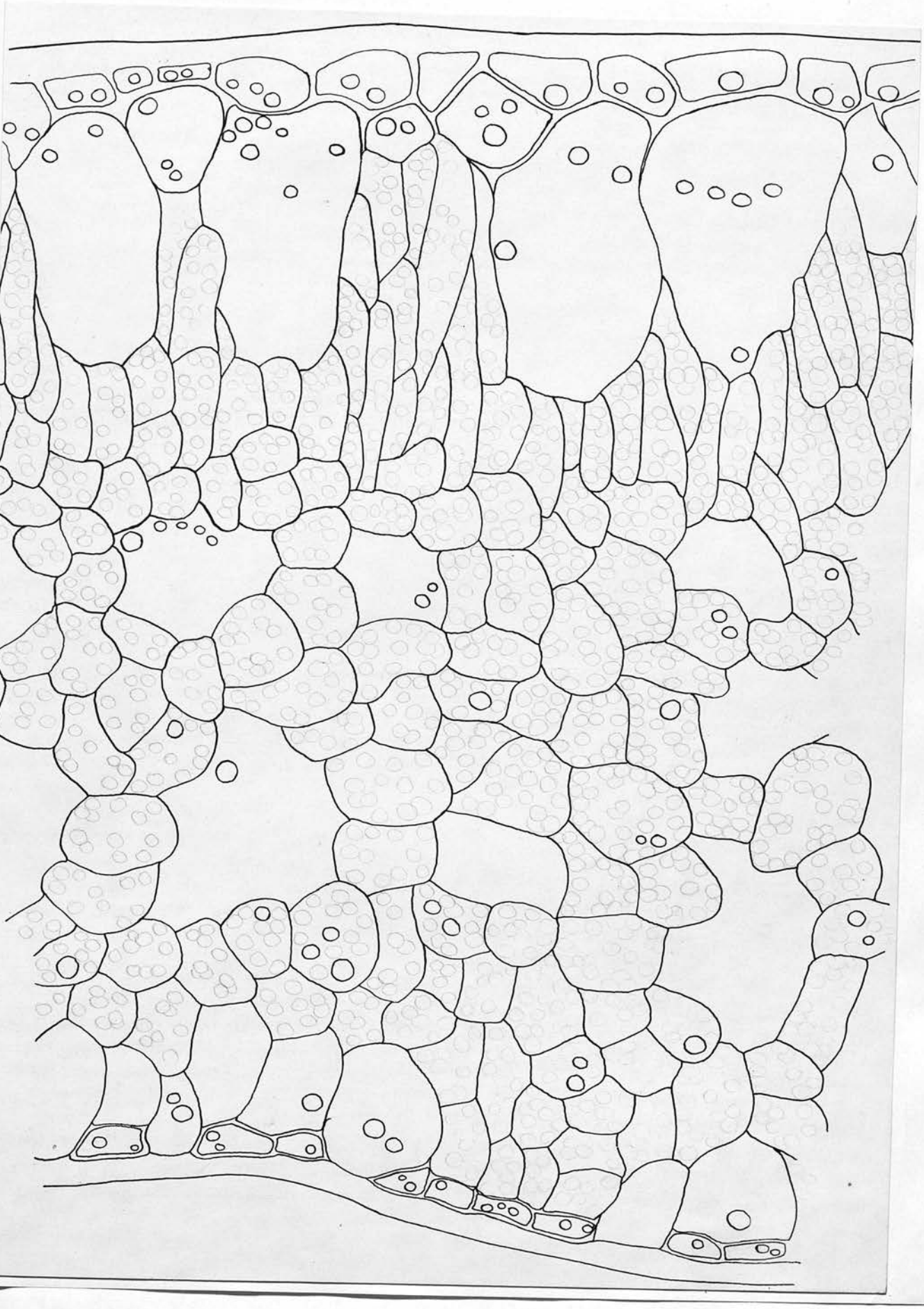


Fig. L . Transverse section of the upper part of a leaf of R. jasminiflorum X(Sybyl) showing greatly enlarged and irregular hypoderm cells and discontinuous epidermal cells, many containing oil droplets: also showing numerous spicular cells in the palisade tissue.

FIGURE L.

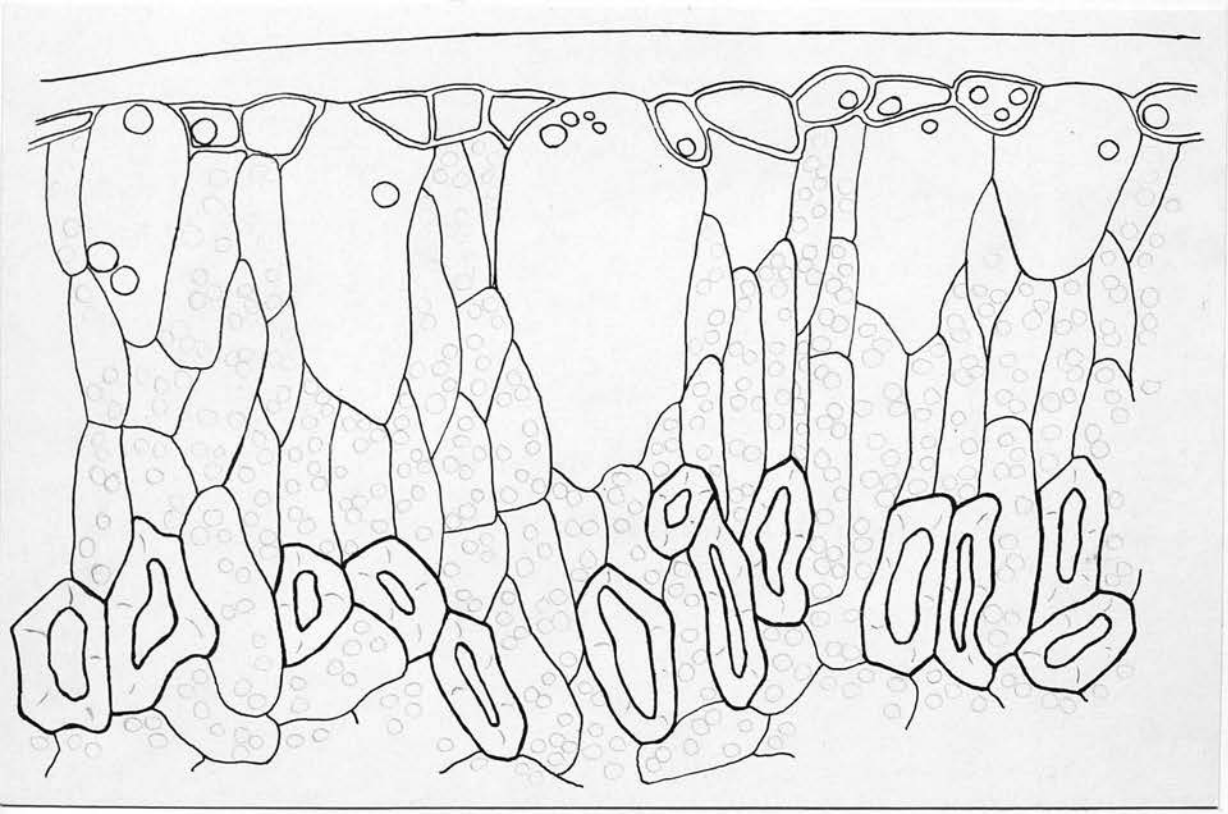


Fig. LI . Transverse section of the upper part of a leaf of R. sino-vaccinioides showing thick-walled pitted epidermal cells and thin-walled irregular hypoderm cells. Camera lucida, x 300.

FIGURE LI.

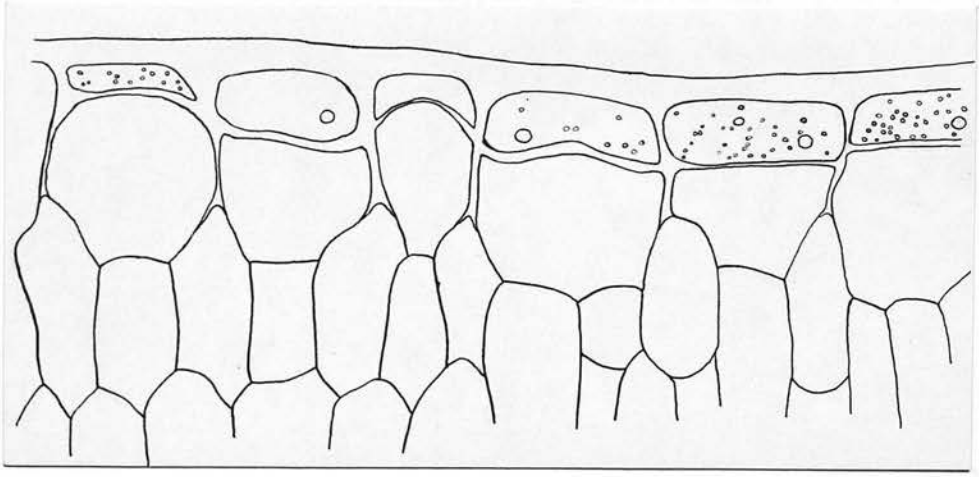


Fig. LII . Transverse section of part of the leaf of R. fictolacteum showing a double-layered hypoderm, two lateral veins, and a "squared" type of spongy mesophyll. Camera lucida x 200.

FIGURE LII.

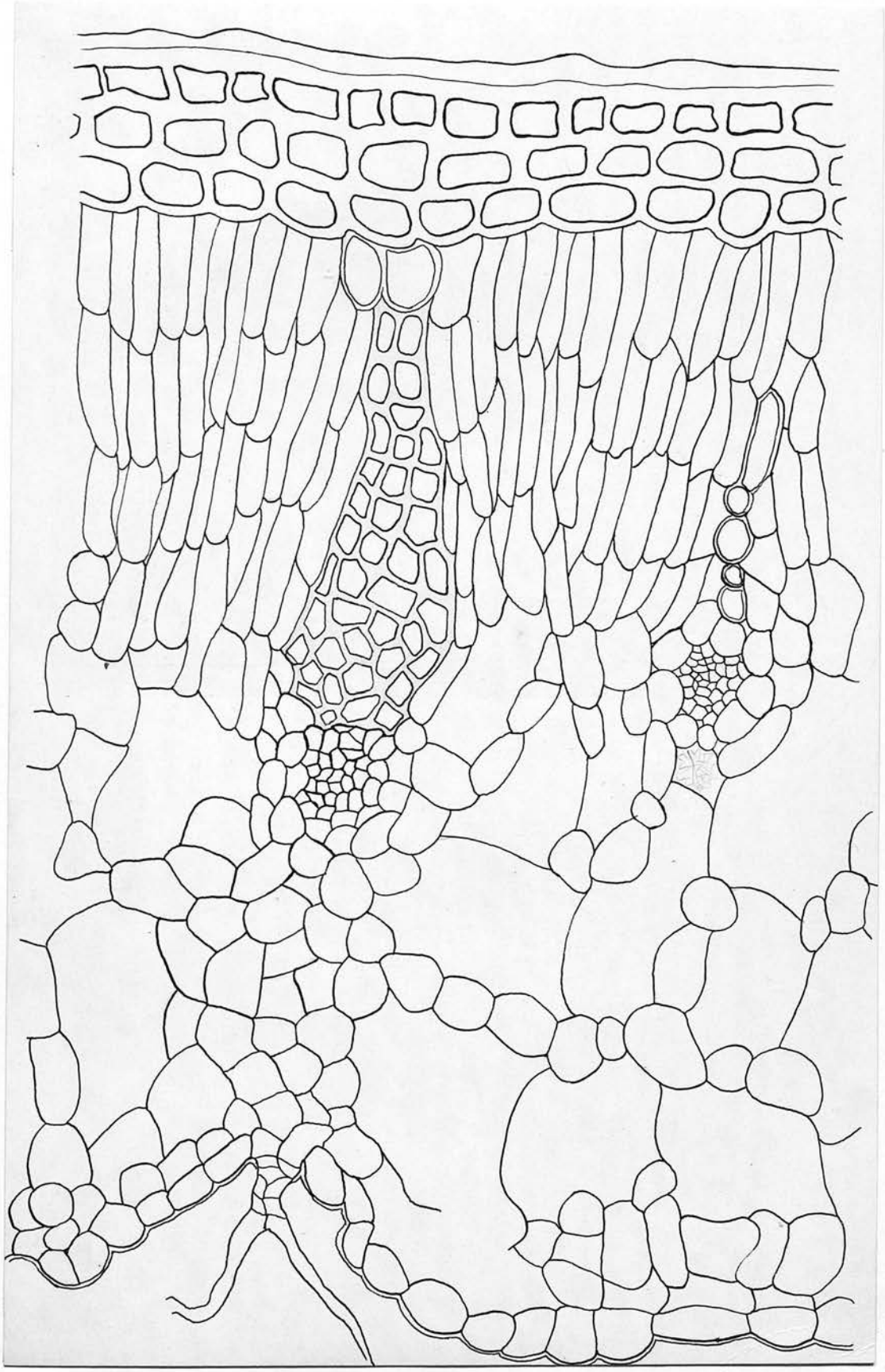


Fig. LIII . Transverse section through part of a leaf of R. giganteum, showing a three-layered hypoderm of large cells, and very slight development of palisade tissue. Camera lucida, x 200.

FIGURE LIII.

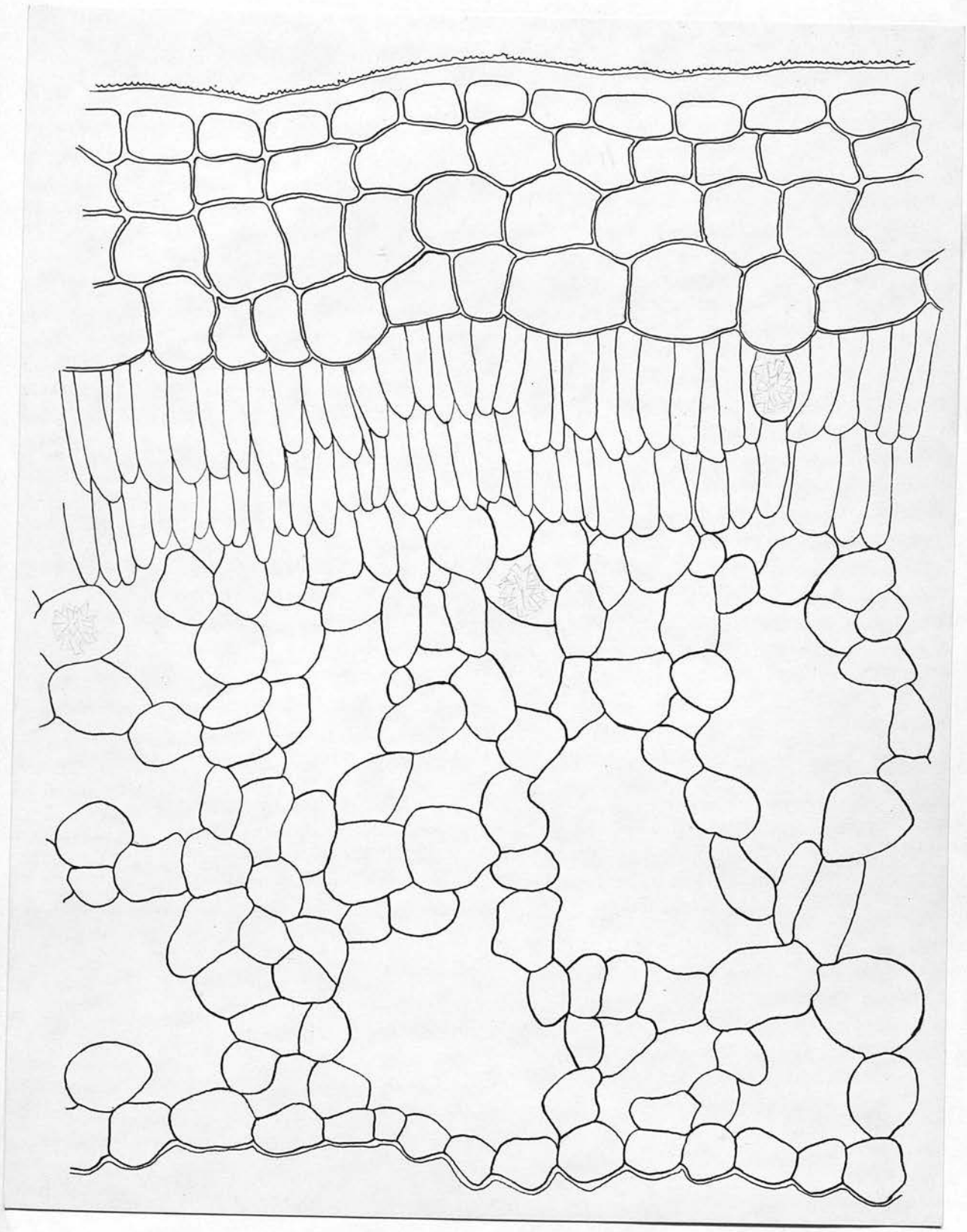


Fig. LIV . Transverse section through a lateral vein in the leaf of R. arboreum, showing the bundle enclosed by a scleren chyma band running from upper to lower epidermis. Note the small palisade and large spongy mesophyll cells. Camera lucida, x 270.

FIGURE LIV.

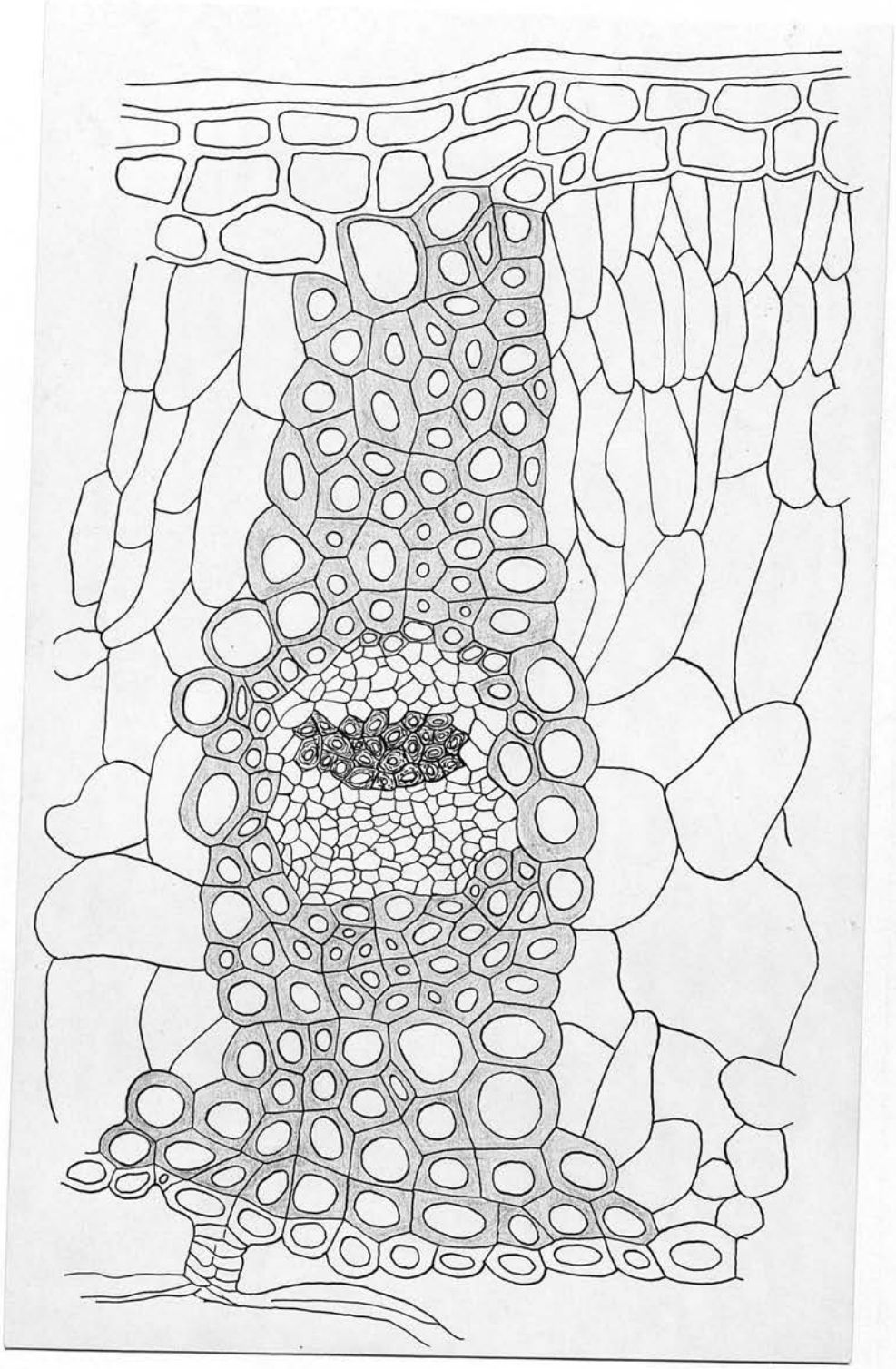


Fig. LV. Transverse section across leaves of (a) R. anthopogon, (b) R. serpyllifolium, (c) R. sino-vaccinioides, showing median bundles. Camera lucida X 30.

FIGURE LV.

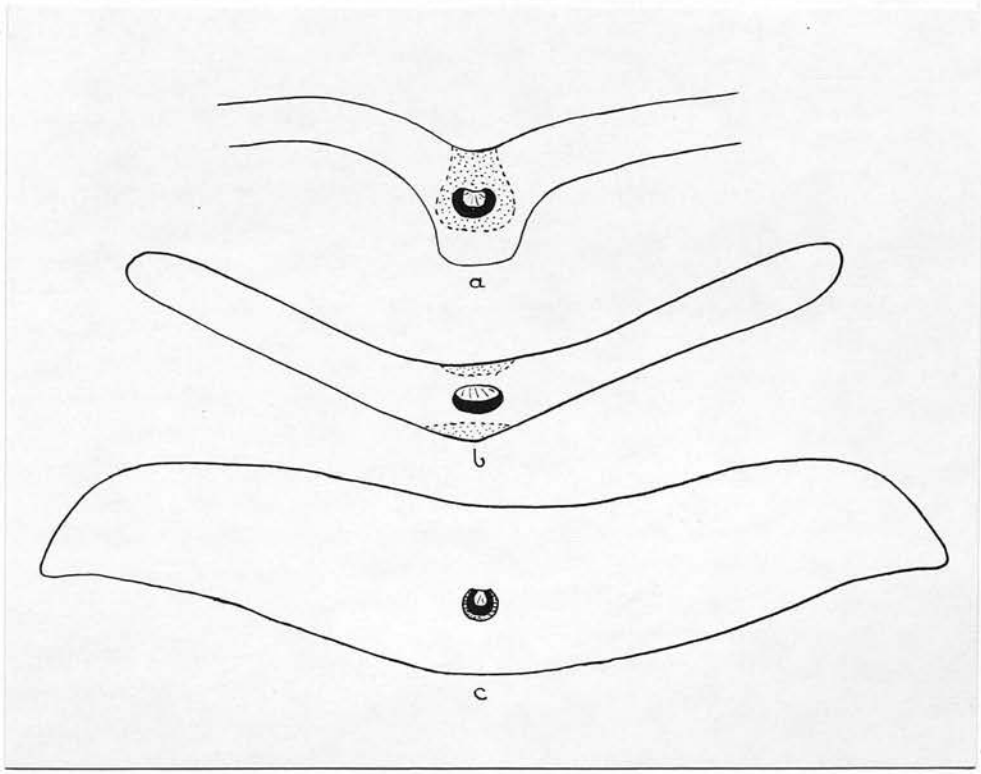


Fig. LVI. Transverse section of part of the stem of R. primulinum, showing broad development of pericyclic cork: c=cortex (dead), f = pericyclic fibres, k = pericyclic cork, p = phloem. Camera lucida X 60.

FIGURE LVI.

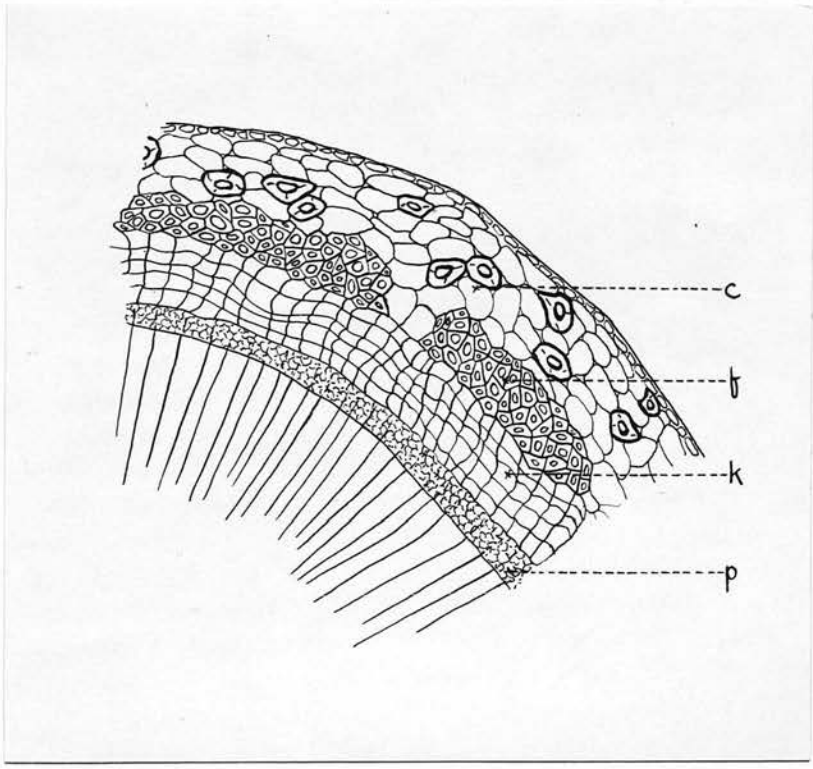


Fig. LVII . Stems of different species of Rhododendron, showing irregular junctions of green living tissue and brown bark. Natural size.

FIGURE LVII.

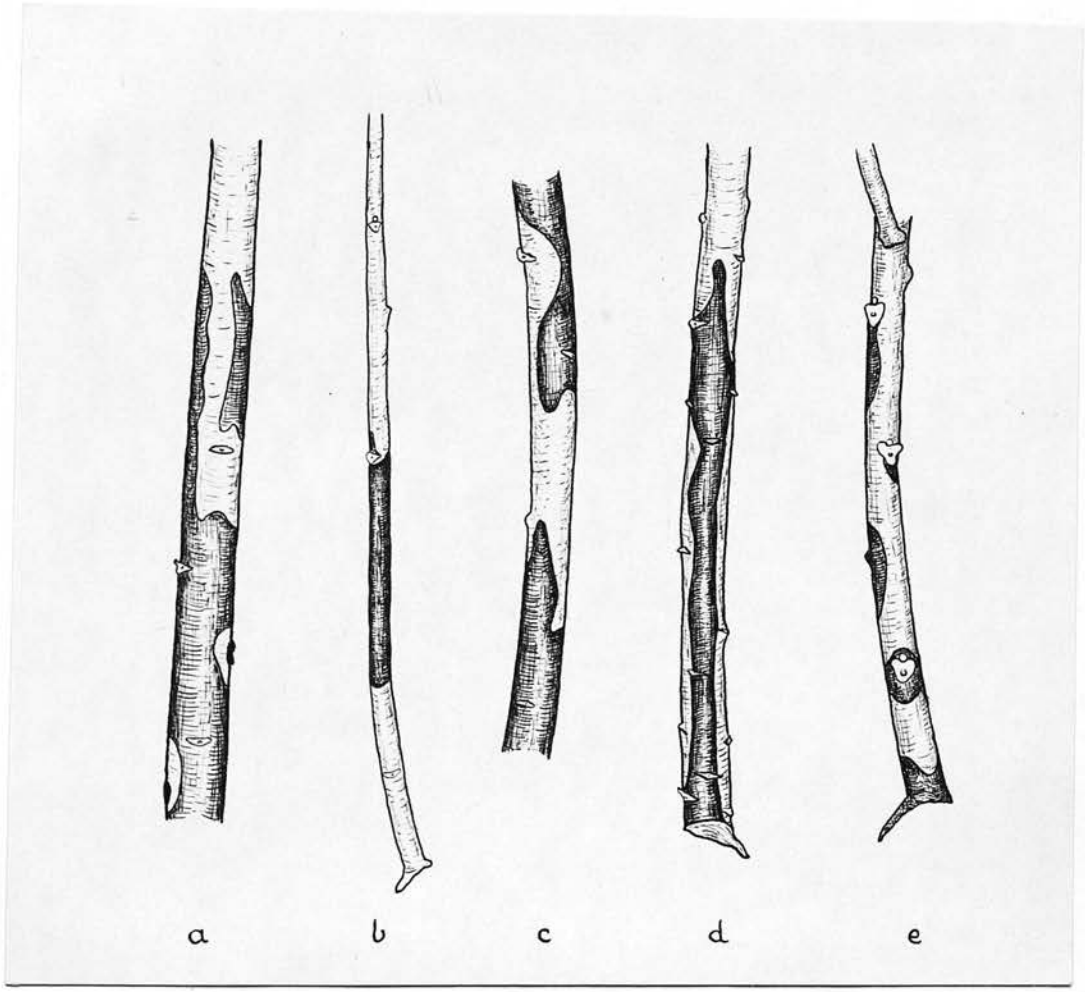


Fig. LVIII . Portion of the stem of R. fulgens, showing suberisation of the cells between and outside the pericyclic fibres: s = suberised pericyclic cells, f = pericyclic fibres, k = pericyclic cork cylinder, s^1 = suberised cortical cells, c = normal cortical cells. Camera lucida, x 340.

FIGURE LVIII.

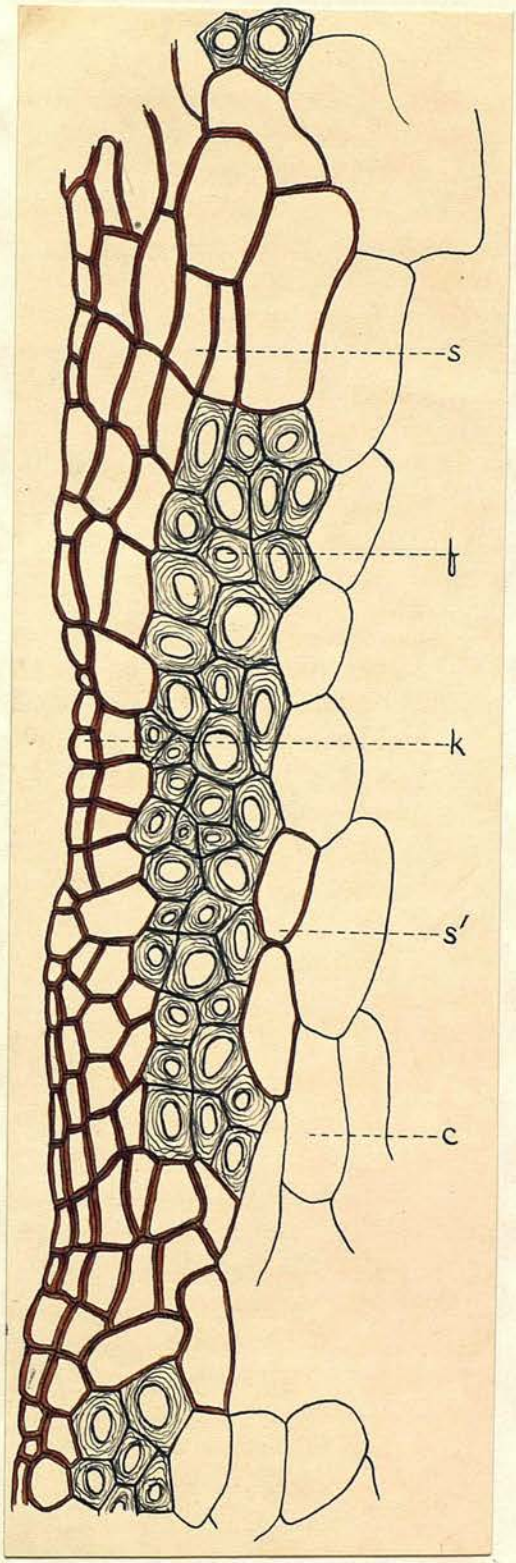


Fig. LIX . Portion of the stem of R. fulgens in transverse section, showing the pericyclic fibres completely enclosed by suberised cells. Camera lucida, x 340.

FIGURE LIX.

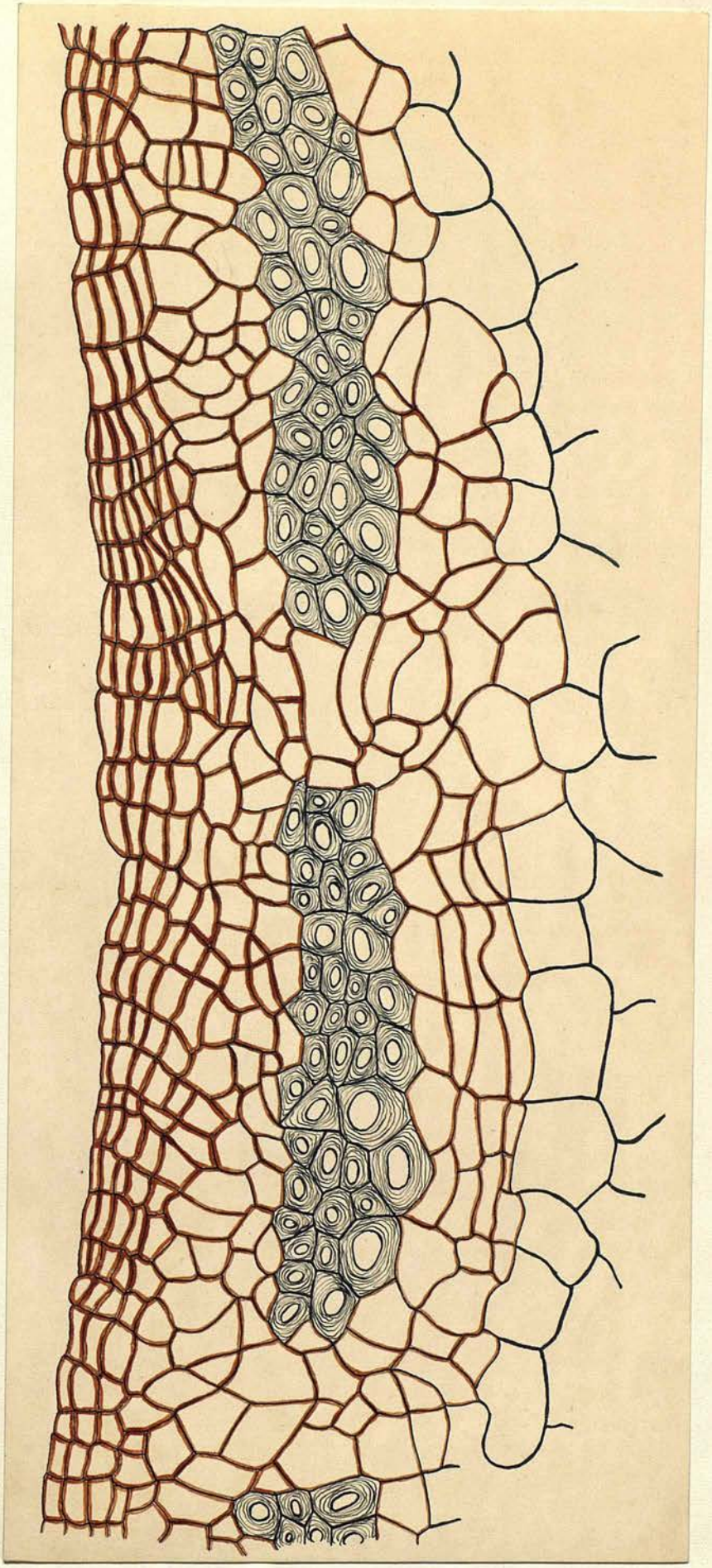


Fig. LX . An advanced stage in cortical cork formation in the stem of R. fulgens: k = pericyclic cork, k^1 = cortical cork, f = pericyclic fibres, c = living cortex, c^1 = dead cortex, e = epidermis. Camera lucida, x 340.

FIGURE LX.

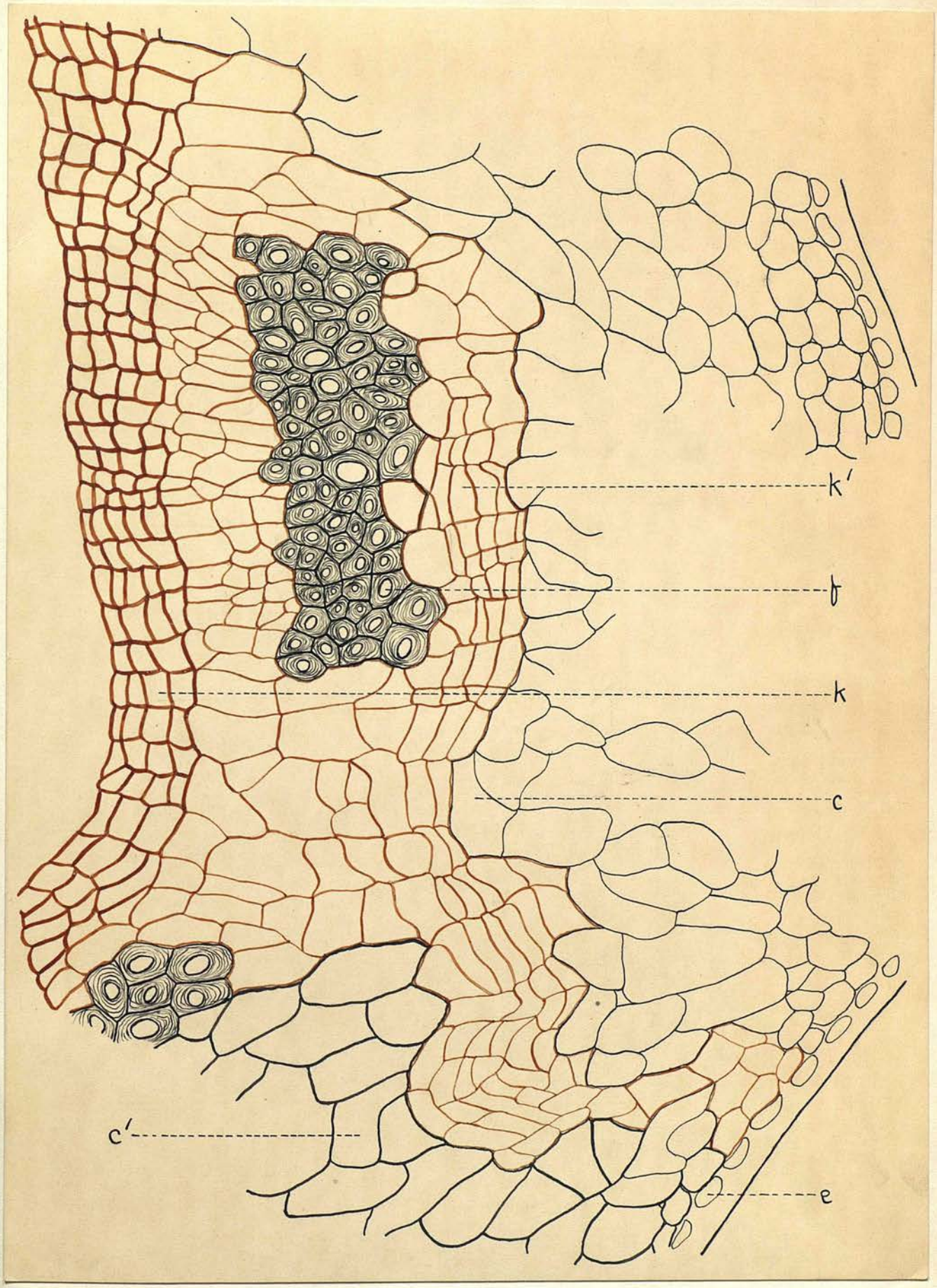


Fig. LXI . A portion of the outer cortex in the stem of R. fulgens, showing division and subsequent suberisation of some of the cortical cells: e = epidermis, s = suberised cortical cells, sc = sclereid. Camera lucida, x 500.

FIGURE LXI.

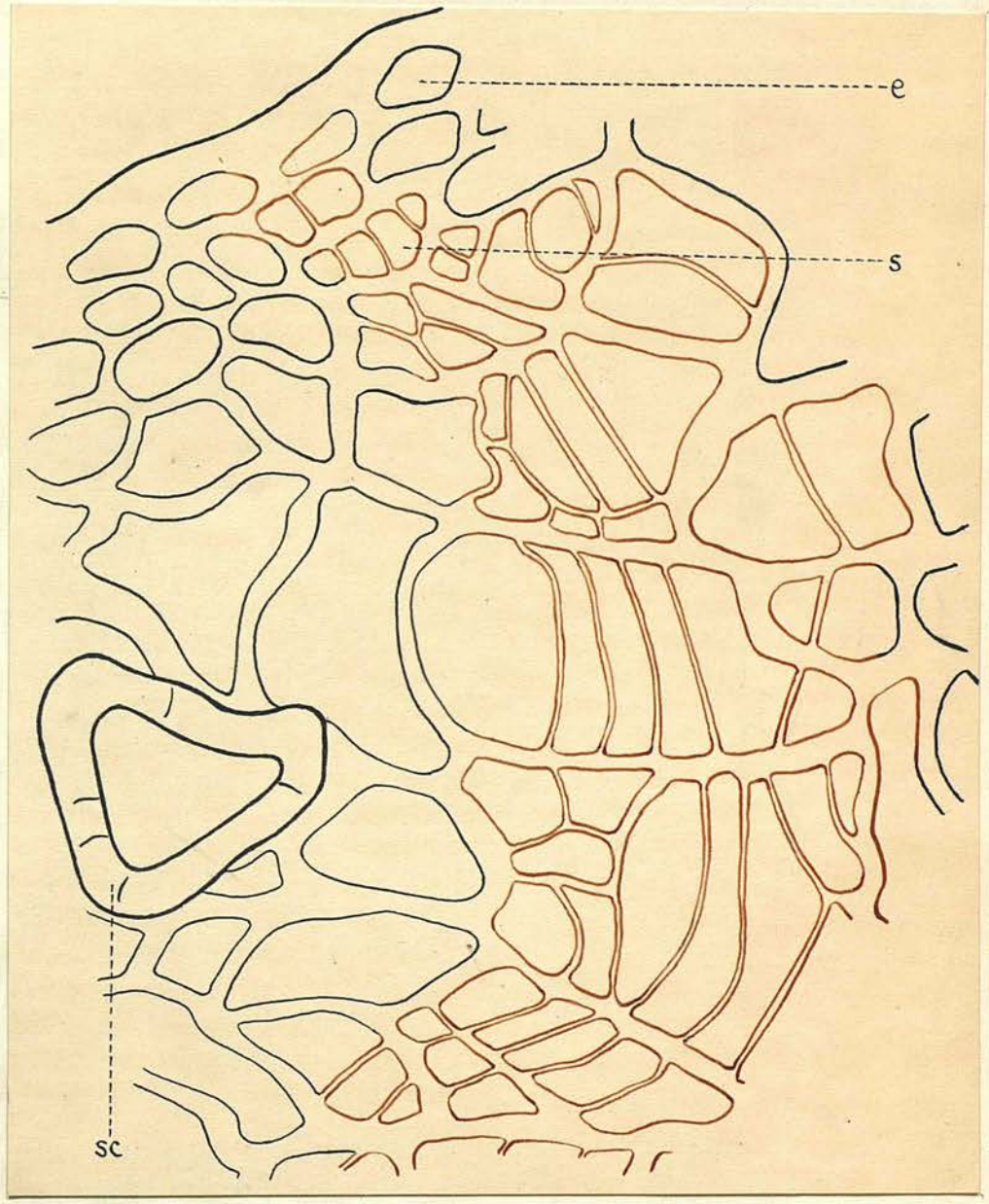
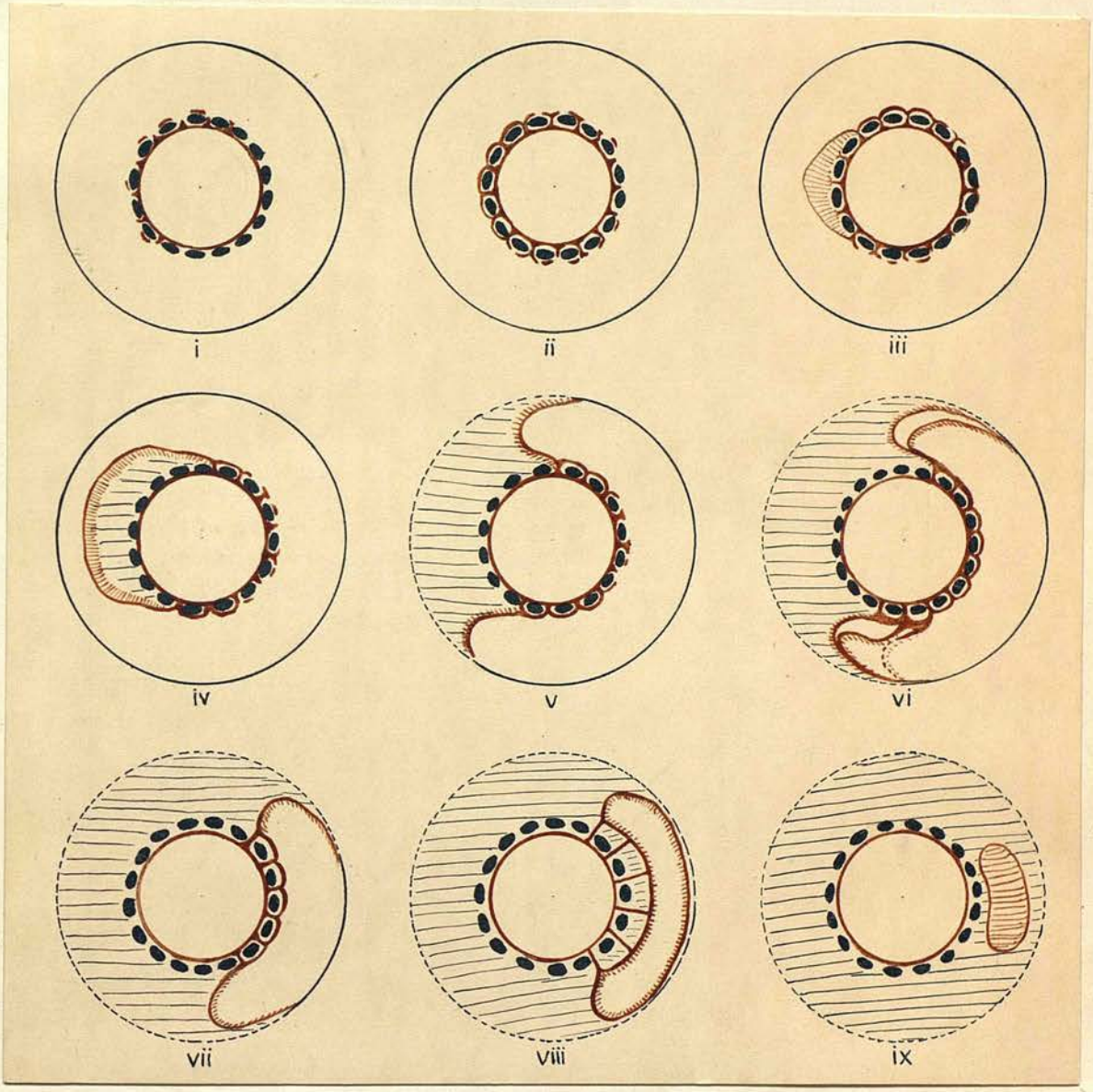


Fig. LXII . Diagrams to represent stages of cortical cork development, passing downward through the stem. Pericyclic fibre masses in black, pericyclic and cortical cork in brown, living cortex white, dead cortex in horizontal lines.

FIGURE LXII.



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Cork Formation in Rhododendron.

By C. Marion Baron.

(Read 16th May 1929.)

The formation of cork in the stem of most species of Rhododendron is of two kinds; firstly of pericyclic and later of cortical origin. The pericyclic cork is formed early in the green stem, usually appearing first behind the gaps between the masses of pericyclic fibres. It quickly forms a cylinder, 2–3 cells wide, of suberised rectangular cells, completely enclosing the stele, often before the pericyclic fibres are fully developed. In a very few species, such as *R. primulinum*, *R. obtusum*, and *R. longistilum*, this cork layer apparently acts as an effective barrier between stele and cortex, the latter being cut off from supply and dying off gradually down the stem. This is evident on the external surface of the stem sometimes as a gradual transition, sometimes as a definite junction of green and brown colour. The species which show only this pericyclic cork appear to be those which possess a very narrow cortex and a particularly early development of cork in the young stem. In *R. primulinum*, for example, the cork layer when fully developed (3–4 cells wide) may measure as much as half the width of the entire cortex, while in large stems, like that of *R. fulgens*, the width of the cork layer is about 1/40th or less of that of the cortex.

This effect, however, produced on the cortex by the pericyclic cork only, seems to be exceptional. The majority of stems show a sharp junction of green living tissue and brown withered bark, usually in the basal part of the last year's growth. This junction runs irregularly round the stem, often extending for several inches up on one side. Below the junction, patches of living green tissue, varying in size, can often be found enclosed in the dead bark. These occur sporadically, sometimes but not necessarily connected with old leaf or bud traces. The bases of the older leaves are often surrounded by similar patches of green tissue where the rest of the stem is brown; these turn brown some time after the leaf has fallen.

Transverse sections taken across the junction from above

downwards show an unusual development of cortical cork. Some time after the pericyclic cork layer is complete, the cells between the pericyclic fibres on one side of the stem, and then those immediately outside them, become lightly suberised (fig. 1, i, and fig. 2). These cells proceed to divide tangentially,

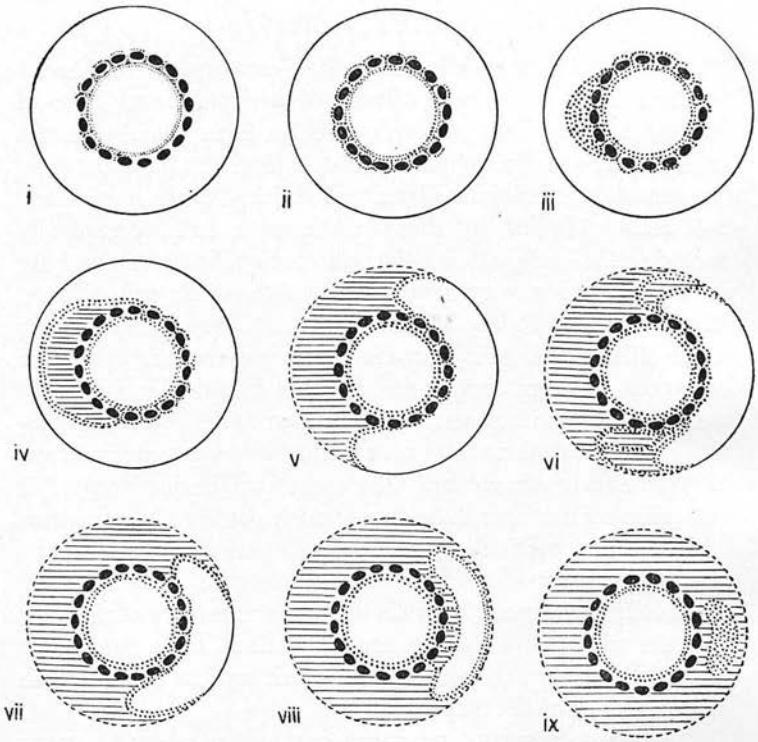

FIG. 1.—Diagram to show stages of cortical cork development, passing down the stem. Pericyclic fibre masses indicated in black, dead cortex in horizontal lines, cork in dotted lines.

and the sclerenchyma masses thus become enclosed on all sides by a layer of cork, 2–3 cells deep (fig. 1, ii). The cortex immediately outside this becomes closer in texture and shows a great accumulation of starch. Passing farther down, almost into the brown portion of the stem, this meristematic activity affects the cortex farther and farther out, until eventually two arcs of cork tissue are formed (fig. 1, iii, iv, and v). These take a curved, oblique course through the cortex from the inner cork cylinder to the epidermis, cutting off between them a mass of

cortex which quickly dies. New phellogen layers arise in the same way in the still living cortex (fig. 1, vi), and each is

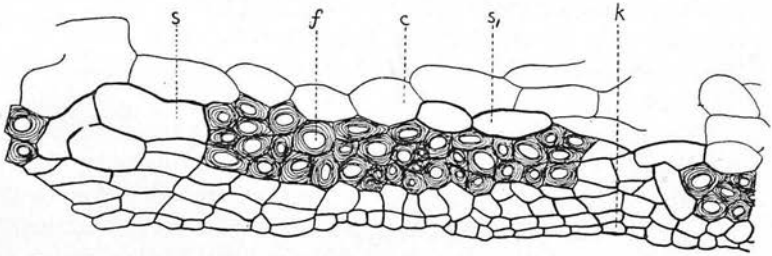

FIG. 2.—Camera lucida drawing, showing suberisation of the cells between and outside the pericyclic fibres.
c=living cortical cells; f=pericyclic fibres; s=suberised pericyclic cells; s_1=suberised cortical cells; k=pericyclic cork cylinder.

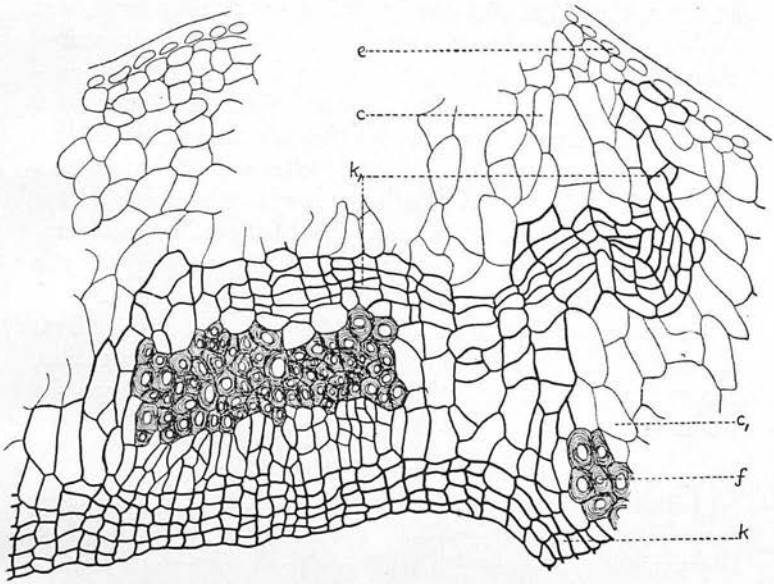

FIG. 3.—An advanced stage in cortical cork formation.
c=living cortex; c_1=dead cortex; k=pericyclic cork; k_1=cortical cork; f=pericyclic fibres; e=epidermis.

accompanied by a heaping up of starch in the adjacent cortical cells. Fresh masses of cortex are thus cut off, until the two phellogen layers meet and coalesce on the opposite side of the stem from which they arose. At this point the whole of the external surface of the stem appears brown, a small patch of

central cortex being the only living tissue left outside the stele (fig. 1, viii). This becomes smaller, and the final stage of meristematic activity is seen in the small patch of suberised cortical cells at the base of the junction. The whole of the cortex below this level is completely dead and devoid of contents.

This method of cork formation in Rhododendron was investigated on account of some work published by Priestley (1) in which he correlated the pericyclic origin of the phellogen in the stem with a functional endodermal barrier, the latter causing accumulation of sap inside the stele and thereby determining the position of any future meristematic activity. In a later paper (2) Priestley expresses the opinion that the pericyclic fibres function in the same way. In Rhododendron, however, the fibres very rarely form a continuous band, and further, the pericyclic cork layer is often completed some time before the fibrous layer. Of greater interest in this connection is the development of several phellogen layers in a cortex which is still green and living for an indefinite time after the completion of the pericyclic cork cylinder. To account for this, two alternatives may be suggested; either the cork cells formed by the pericyclic phellogen are not completely impermeable, or else the extent of conduction in the cortical cells is greater than has hitherto been supposed.

My thanks are due to Professor Wright Smith, of the Royal Botanic Garden, for providing facilities for this investigation, and to Dr. Graham for invaluable suggestions throughout the work.

References.

(1) Priestley, J. H., and Woffenden, Lettice M. (1922): New Phytologist, xxi, 252–268.

(2) —— (1926): Proc. Leeds Phil. Soc., i, pt. iii, 123–135.